



## The phylum Cnidaria: A review of phylogenetic patterns and diversity 300 years after Linnaeus\*

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\*In: Zhang, Z.-Q. & Shear, W.A. (Eds) (2007) Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. *Zootaxa*, 1668, 1–766.

### Table of contents

Abstract	128
The Linnaean perspective on Cnidarian diversity	128
Modern perspectives on Cnidarian diversity	129
PHYLUM CNIDARIA	129
CLASS ANTHOZOA: M. Daly, C. S. McFadden & D. G. Fautin	130
SUBCLASS HEXACORALLIA: M. Daly & D. G. Fautin	130
Order Actiniaria: E. Rodríguez, M. Daly, & D. G. Fautin	313
Order Antipatharia: S. C. France, M. Brugler & D. Opresko	136
Order Ceriantharia: M. Daly	138
Order Corallimorpharia: M. Daly & D. G. Fautin	139
Order Scleractinia: S. L. Romano & J. L. Stake	140
Order Zoanthidea: M. Daly	143
SUBCLASS OCTOCORALLIA: C. S. McFadden	144
Order Alcyonacea	145
Order Helioporacea	149
Order Pennatulacea	150
CLASS CUBOZOA: A.G. Collins	151
Order Carybdeida	151
Order Chirodropida	152
CLASS HYDROZOA: P. Cartwright & A. G. Collins	153
SUBCLASS HYDROIDOLINA	153
Order Anthoathecata	153
Order Leptothecata	159

Order Siphonophorae	163
SUBCLASS TRACHYLINA	165
Order Actinulida	165
Order Limnomedusae	166
Order Narcomedusae	167
Order Trachymedusae	168
CLASS SCYPHOZOA: M. N. Dawson	168
Order Coronatae	169
SUBCLASS DISCOMEDUSAE	170
Order Semaestomeae	170
Order Rhizostomeae	170
CLASS STAUROZOA: A. G. Collins	171
Order Stauromedusae	171
Acknowledgements	173
References	173

## Abstract

Systema Naturae includes representatives of every major lineage of the animal phylum Cnidaria. However, Linnaeus did not classify the members of the phylum as is now done, and the diversity of the group is not well represented. We contrast the Linnaean perspective on cnidarian diversity with the modern, phylogenetic perspective. For each order, we detail diversity at the family level, providing phylogenetic context where possible.

**Key words:** Systematics, black coral, coral, hydroid, jellyfish, octocoral, sea anemone

## The Linnaean perspective on Cnidarian diversity

The phylum Cnidaria is a diverse group of relatively simple animals united by the ability to synthesize a highly complex cellular product, the cnida. Its members, which include corals, hydroids, jellyfishes, sea anemones, and sea fans, are abundant and common in marine environments, and have been known to natural historians for millennia.

Linnaeus (1758) included representatives of all major cnidarian lineages in Systema Naturae in various orders of Vermes Imperfecta. His taxonomic placement of cnidarian species was based largely on whether they were solitary or colonial, and whether they had no skeleton, a stony skeleton, or a proteinaceous skeleton. Linnaeus' Mollusca included three genera with members that are now considered part of Cnidaria: *Priapus*, *Holothuria*, and *Medusa*. Like all members of his Mollusca, these animals have relatively uniform bodies and lack a skeleton. *Priapus* was defined as having a fixed base and a terminal orifice, characteristics common to many sessile animals; the Linnaean species *equinus* remains in use as *Actinia equina*, the type species of the actinarian sea anemone genus *Actinia* (see Williams *et al.* 1982). Linnaeus' *Holothuria* included free-swimming forms with a humped body and tentacles of unequal length and number; this genus includes the hydrozoan *Physalia physalis*, described by Linnaeus (1758) as *Holothuria physalis*. Members of the genus *Medusa* share a pelagic, gelatinous body with a central mouth on the lower surface. This genus includes all of the Linnaean species now assigned to Scyphozoa and Cubozoa. Common hydrozoans, such as the blue button *Porpita porpita* and the by the wind sailor *Verella velella*, were also included in this genus. Not all species of *Medusa* are cnidarians, however: *Medusa beroe* is clearly a member of the ctenophore genus *Beroe*, although identity of the Linnaean species is unclear (Bayha *et al.* 2004). The genus *Priapus* was suppressed for Cnidaria in Opinion 1295 of the International Commission on Zoological Nomenclature (Bulletin of Zoological Nomenclature 42:34–36; April 1985): it has been ruled to belong to phylum Priapulida.

Lithophyta and Zoophyta are distinguished from Mollusca in being colonial. Members of Lithophyta have a hard skeleton; those of Zoophyta have no skeleton, or a flexible one. The lithophytes are a heterogeneous assemblage of hydrozoan corals (e.g., *Millepora*), octocorals (e.g., *Tubipora*), scleractinian corals (e.g., *Madrepora*), and bryozoans. Zoophyta is likewise heterogeneous, including the hydrozoans *Hydra* and *Tubularia*, and several groups now classed in Octocorallia, including *Isis*, *Gorgonia*, and *Pennatula*. Although these names remain in use and are valid for particular cnidarian genera, Linnaeus' (1758) concept of each does not correspond to modern use. For example, *Gorgonia* includes taxa now recognized as belonging to the anthozoan subclass Octocorallia (e.g., the gorgonian *Gorgonia flabellum*) and to its sister subclass, Hexacorallia (e.g., *Gorgonia spiralis*, now the black coral *Cirripathes spiralis*). *Hydra* includes species belonging to groups other than Cnidaria (e.g., the ciliate *Epistylis digitalis*, described as *Hydra digitalis*). *Millepora* includes at least one scleractinian coral (*Millepora damicornis*, now *Pocillopora damicornis*).

Although Linnaeus (1758) recognized the breadth of diversity now encompassed in Cnidaria, none of the higher-level distinctions made in *Systema Naturae* correspond to modern taxonomic groups. The cnidarians classified together in Mollusca, Lithophyta, or Zoophyta are, by and large, only distantly related. All of the Linnaean categories include representatives of at least two classes, and Mollusca includes three: the anthozoan *Actinia equina*, the hydrozoan *Physalia physalis*, and the scyphozoan *Aurelia aurita*. Nonetheless, the characters Linnaeus used to differentiate taxa are commonly used to recognize groups within lineages, and their importance and applicability remain the focus of taxonomic and phylogenetic discussion (e.g., France *et al.* 1996; Berntson *et al.* 1999; Daly *et al.* 2003; Marques & Collins 2004; Dunn *et al.* 2005; Medina *et al.* 2006; McFadden & Alderslade 2007).

## Modern perspectives on Cnidarian diversity

### PHYLUM CNIDARIA

Cnidaria comprises two reciprocally monophyletic clades. The distinction between Anthozoa and Medusozoa is well-supported by anatomy and life history (Salvini-Plawen 1978; Bridge *et al.* 1995), genome structure (Bridge *et al.* 1992; but see Brugler 2004 for unusual cerianthid genome), and DNA sequences (e.g., Cavalier-Smith *et al.* 1996; Odorico & Miller 1997; Collins 1998; Berntson *et al.* 1999; Kim *et al.* 1999; Medina *et al.* 2001; Won *et al.* 2001; Collins 2002). The traditional taxonomic structure of Cnidaria mirrors its phylogenetic structure, although the ranks of many groups are incompatible with their hierarchical phylogenetic position. For instance, the class Anthozoa comprises all members of the clade Anthozoa; its sister taxon, Medusozoa, comprises the remaining classes. Thus, class and other ranks have different phylogenetic implications across the phylum.

Cnidae, organelle-like capsules with eversible tubules (e.g., Weill 1934; Watson 1988), are the diagnostic feature of the phylum. Of the three types of cnidae (nematocysts, ptychocysts, and spirocysts), only nematocysts are found across the clade. All cnidarians possess cnidae; no loss of the feature has been documented. Three other features sometimes considered to be diagnostic of Cnidaria are radial symmetry and planula and polyp stages in development, but all are problematic. Although many cnidarians exhibit radial symmetry, some are directionally asymmetric (Dunn & Wagner 2006), and many have a biradial or bilateral organization, leading some to conclude that bilateral symmetry is the ancestral condition for the phylum (Salvini-Plawen 1978; Matus *et al.* 2006). Furthermore, the other two features are difficult to define. For example, the motile stage between embryo and settled juvenile in any given cnidarian's life cycle is typically termed a planula, and, although this stage is usually ciliated, sausage-shaped, and non-feeding, deviations from this pattern – e.g., *Halicystus* (class Staurozoa), *Hydra* (class Hydrozoa), *Zoanthidea* (class Anthozoa)—have been well documented. Polyp forms are even more variable than planulae, being solitary or colonial; if colonial, polyps

may be monomorphic or polymorphic; they may or may not have a mineralized skeleton; they may be benthic or pelagic; and tentacles, although commonly present, may be absent.

We summarize the current state of knowledge of the membership of classes and orders of cnidarians, with brief notes on families. The most recent coverage of the phylum at these levels was by Dunn (1982).

## **CLASS ANTHOZOA**

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The class Anthozoa comprises two reciprocally monophyletic lineages, Octocorallia and Hexacorallia. All members of Anthozoa are exclusively polypoid, and may be colonial, clonal, or solitary, skeleton-less or with a mineralic and/or proteinaceous skeleton. Anthozoa currently contains approximately 7,500 extant species.

Although an early phylogeny based on fragments of 18S rDNA from a relatively small subset of Cnidaria found Anthozoa to be paraphyletic with respect to a monophyletic Medusozoa, this result was interpreted as an artifact of analytical methods and the taxon sample because Anthozoa was recovered as a clade under some analytical parameters and when additional data and taxa were considered (Bridge *et al.* 1995). Subsequent studies of larger rDNA datasets (France *et al.* 1996; Odorico & Miller 1997; Song & Won 1997; Berntson *et al.* 1999; Collins 2002) support anthozoan monophyly. Phylogenetic analyses of morphological data (e.g., Won *et al.* 2001) also have corroborated this hypothesis, and have suggested at least three diagnostic apomorphies for Anthozoa: actinopharynx, siphonoglyph, and mesenteries. The actinopharynx (= stomadeum, gullet) is an ectoderm-lined tube that projects into the gastrovascular cavity (= coelenteron); this structure is found in all Anthozoa, with one known exception, the black coral *Sibopathes* (Opresko 1993). The siphonoglyph (= sulcus) is a densely ciliated, often more highly glandular region of the actinopharynx; it is single, paired, or, rarely, absent (e.g., in ptychodactarian sea anemones; the presence of a siphonoglyph in antipatharians is disputed), and in asexually-derived individuals, there may be more than two. The siphonoglyph reflects the plane of bilateral symmetry for the polyp (Finnerty *et al.* 2004). Bilateral symmetry is further defined by the mesenteries (the term septa, which has been used for these structures, should be reserved for the calcareous radial partitions secreted by the mesenteries of scleractinians: Bayer *et al.* 1983), radially-arrayed sheets of tissue that extend all or part of the way from the body wall to the actinopharynx. Unlike the gastric septa of Staurozoa, at least some of the mesenteries extend nearly halfway across the gastrovascular cavity, from the body wall and to the actinopharynx. Mesenteries are arranged in cycles (members of each cycle form more or less simultaneously) and bear the gametogenic tissue and epitheliomuscular cells that are concentrated as retractor muscles. The free edge of a mesentery is typically elaborated into a mesenterial filament with abundant gland cells, nematocysts, and cilia. The exclusively polypoid nature of the anthozoan life cycle is sometimes considered a synapomorphy for the group (e.g., Hyman 1940; Brusca & Brusca 1990), but this attribute is shared with at least some medusozoans and may be a plesiomorphy (Collins *et al.* 2006a).

## **SUBCLASS HEXACORALLIA**

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The anthozoan subclass Hexacorallia comprises all scleractinian and black corals, tube anemones, and sea anemones in the broadest sense (i.e., orders Actiniaria, Antipatharia, Ceriantharia, Corallimorpharia, Scleractinia, and Zoanthidea). Hexacorallia currently contains about 4,300 extant species (Doumenc & van Praët 1987). As the name suggests, most hexacorallians have hexamerous symmetry, although eight- or ten-part symmetry are not uncommon. All members of Hexacorallia have spirocysts, a type of cnida with a single-walled capsule and a tubule composed of tiny entangling sub-threads (Mariscal *et al.* 1977).

Because the morphology of hexacorallian polyps is more variable than that of octocorallian polyps, monophyly of the group and relationships within it have been difficult to interpret. Based on similarities in morphology between the cerinula larvae of the cerianthid *Arachnactis* and the antipatharian polyp, Antipatharia and Ceriantharia have been separated from the remaining orders as a distinct subclass, Ceriantipatharia (see van Beneden 1897; Hyman 1940; Wells & Hill 1956; Berntson *et al.* 1999). France *et al.* (1996), Berntson *et al.* (1999), and Brugler and France (2007) addressed the placement of Ceriantharia and Antipatharia explicitly, and determined that Ceriantharia and Antipatharia are not sister taxa: Ceriantharia is sister to (or the basal member of) Hexacorallia, within which Antipatharia nests. Other studies of hexacorallian relationships corroborate these conclusions (Berntson *et al.* 2001; Won *et al.* 2001; Daly *et al.* 2002, 2003). Two phylogenies based on 18S rDNA (Song *et al.* 1994; Song & Won 1997) found support for excluding Ceriantharia from Hexacorallia, but this seems to have been an artifact of their relatively small sample size because subsequent studies of 18S that included more taxa concluded that Ceriantharia is the basal-most lineage within Hexacorallia (Berntson *et al.* 2001; Won *et al.* 2001; Daly *et al.* 2002, 2003).

Most molecular phylogenetic analyses support monophyly of each of the extant hexacorallian orders, although the relationship between Scleractinia and Corallimorpharia is controversial. Nuclear data (Won *et al.* 2001; Daly *et al.* 2002, 2003) support Corallimorpharia as the sister-group to a monophyletic Scleractinia, but analyses of mitochondrial genes suggest that Corallimorpharia nests within Scleractinia (France *et al.* 1996; Romano & Cairns 2000; Medina *et al.* 2006). This may be the result of relatively limited taxon samples in the analyses of mitochondrial sequences: a study by Brugler and France (2007) that expanded the sample of Medina *et al.* (2006) to include an antipatharian and a zoanthidean found that Corallimorpharia and Scleractinia are reciprocally monophyletic sister taxa. Chen *et al.*'s (1995) analysis of a very small fragment of 28S rDNA suggested that Corallimorpharia is more closely related to a subset of Actiniaria, but these authors did not recover this topology in subsequent analysis of a more extensive data set (Veron *et al.* 1996). The putative order Ptychodactiaria has been subsumed within Actiniaria, based on morphological (Cappola & Fautin 2000) and molecular (Berntson *et al.* 1999; Daly *et al.* 2003) evidence. Questions of monophyly aside, relationships among the orders are unclear. The relationship between Actiniaria and Zoanthidea is poorly resolved in all phylogenetic studies of molecular data (e.g., Daly *et al.* 2002, 2003; Brugler & France 2007). However, most analyses agree that Actiniaria, Antipatharia, Corallimorpharia, Scleractinia, and Zoanthidea constitute a clade, with Ceriantharia as its sister group.

#### Order Actiniaria

E. Rodríguez, M. Daly, & D. G. Fautin

The order Actiniaria Hertwig, 1882 comprises soft-bodied, solitary polyps with tentacles that are not pinnate, and arise at the margin and/or from the disc. These attributes are seen in some members of other hexacorallian orders, raising concern that Actiniaria is not monophyletic (e.g., Stephenson 1921; Schmidt 1972, 1974). Although no published genetic studies have explicitly addressed relationships among actinarians, all broad-scale analyses of hexacorallian or anthozoan phylogeny (e.g., Berntson *et al.* 1999; Won *et al.* 2001; Daly *et al.* 2002, 2003) have included multiple actinarians, and nearly all have demonstrated monophyly of the order. A notable exception is the analysis by Chen *et al.* (1995) of 28S rDNA, which found Actiniaria polyphyletic with respect to Corallimorpharia and Scleractinia; this result was based on a very small fragment of DNA, and has not been seen in subsequent analyses.

Currently, Actiniaria comprises approximately 1,200 species in 46 families. Its members are found at all depths, in all oceans, and in many estuaries. The current classification for Actiniaria is based on that of Carlgren (1949), who recognized three suborders: Endocoelelantheae, Nynantheae, and Protantheae. Nynantheae is the only suborder to comprise more than two families; it was further divided by Carlgren into three "tribes"

(actually infraorders) and three “subtribes” (actually superfamilies). This classification was not intended to reflect phylogeny, and does not: at least some of the nyantheae infraorders are paraphyletic (e.g., Berntson *et al.* 1999; Daly *et al.* 2002, 2003).

Actiniarian families are characterized by the types and distribution of nematocysts; they can be distinguished based on polyp structure, including the morphology and development of musculature, number and arrangement of mesenteries, arrangement and morphology of tentacles, and presence of specialized structures such as acontia. Although nematocyst distribution is used to define some actiniarian taxa, the value of these data for differentiating species or higher taxa has been questioned (Fautin 1988). Several classifications of nematocysts have been proposed (e.g., Schmidt 1972; Mariscal 1974; England 1991; Östman 2000), leading to conflicting diagnoses of the cnidom in some taxa. Furthermore, although all systems of classification for cnidae determine type based on the morphology of the tubule of discharged capsules, for most groups, cnidom has been assessed mainly with undischarged capsules from preserved specimens, making assessment of cnida morphology tentative at best (e.g., Fautin submitted). Polyp anatomy is less controversial, but may be no less problematic: features of taxonomic value, including acrorhagi, marginal sphincter musculature, and reproductive morphology have been the subject of re-evaluation or are difficult to distinguish in a few critical instances (e.g., Riemann-Zürneck 1980; Fautin 1984; England 1987; Cappola & Fautin 2000; Daly & den Hartog 2004). Few families have been the focus of phylogenetic study, and monophyly is unclear for most groups. Furthermore, lack of type material and inadequate species descriptions mean that many species cannot be reliably identified, necessitating the redescription of species and establishment of neotypes. The chapter in this volume by Fautin *et al.* (2007) covers the genera of Actiniaria and Corallimorpharia.

#### *Included families*

**Aiptasiomorphidae Carlgren, 1949** is a monogeneric family comprising four valid species (Carlgren 1949; Fautin 2007). The family is distinguished by the absence of certain types of nematocysts in the tentacles and relatively weak musculature rather than any uniquely present attribute, so may not be monophyletic.

**Acontiphoridae Carlgren, 1938** comprises four genera and fewer than 10 valid species (Fautin 2007). The family is distinguished by the lack of a marginal sphincter rather than any uniquely present attribute, so may not be monophyletic.

**Actinernidae Stephenson, 1922** comprises four genera and approximately 10 species (Carlgren 1949; Fautin 2007). Actinernidae belongs to a distinctive suborder of Actiniaria distinguished by an unusual arrangement of mesenteries; it is differentiated from all other members of the Endocoelelantheae in lacking microcnemes and in having two siphonoglyphs. The polarities of the diagnostic attributes are unclear, rendering assessment of its probable monophyly difficult.

**Actiniidae Rafinesque, 1815** comprises 44 genera and more than 200 valid species (Carlgren 1949; Fautin 2007). Actiniidae is likely not monophyletic. The diagnosis of the family does not include any attribute not seen in other Actiniaria, and studies of DNA sequences that include exemplars from Actiniidae and those from other families in Endomyaria have failed to recover its members as sister taxa (Daly *et al.* 2003; *contra* McCommas *et al.* 1991).

**Actinodendridae Haddon, 1898** comprises three genera and approximately 10 valid species (Ardelean 2003; Fautin 2007). Phylogenetic analysis of morphological attributes indicates that Actinodendridae is monophyletic (Ardelean 2003); its members are united in having the oral disc drawn out into long arm-like lobes bearing dendritic tentacles and in lacking a marginal sphincter.

**Aiptasiidae Carlgren, 1924** comprises five genera and approximately 20 valid species (Carlgren 1949; Fautin 2007). Aiptasiidae is distinguished by the types of nematocysts in the acontia and the relatively weak musculature of the sphincter; because these attributes are also present in several other families, Aiptasiidae may not be monophyletic.

- Actinoscyphiidae Stephenson, 1920** comprises eight genera and approximately 10 valid species, most of which live in deep-sea and chemosynthetic habitats (Sanamyan & Sanamyan, 2007; Rodríguez *et al.* submitted). Phylogenetic analysis of morphological data (Rodríguez *et al.* submitted) indicates that Actinoscyphiidae is monophyletic, but its membership is likely to change as its close ally, Actinostolidae, is revised.
- Actinostolidae Carlgren, 1893** comprises 19 genera and approximately 70 valid species, most of which are from deep-sea and polar waters (Fautin & Hessler 1989; Fautin 2007; Rodríguez *et al.* submitted). The family is distinguished by no acontia and a mesogleal marginal sphincter rather than any unique attribute. A recent phylogenetic analysis of morphological data indicated that this family is not monophyletic (Rodríguez *et al.* submitted).
- Aliciidae Duerden, 1895** comprises five genera and approximately 10 valid species (Fautin 2007). The family is characterized by outgrowths in the column containing macrobasic amastigophores, ectodermal longitudinal muscles in the column, and either no marginal sphincter or a weak one. Schmidt (1974) hypothesized, based on morphology and cnidae, that Aliciidae is closely related to Boloceroiidae.
- Andresiidae Stephenson, 1922** is a monospecific family whose sole species is from the sublittoral of the Mediterranean Sea and surrounding waters (Fautin 2007). This family is characterized by a burrowing habit, an endodermal sphincter, 24 pairs of perfect mesenteries, 24 long, sometimes-deciduous tentacles, and no basilar muscles.
- Andvakiidae Danielssen, 1890** comprises two genera and fewer than five species (Carlgren 1949; Fautin 2007). Andvakiidae is acontiate, with two kinds of nematocysts in the acontia, and its members have a mesogleal sphincter; it thus resembles families Isophelliidae, Sagartiidae, and Sagartiomorphidae, from which it is distinguished by lacking basilar muscles.
- Bathypheiliidae Carlgren, 1932** comprises four genera and eight valid species (Fautin 2007). Riemann-Zürneck (1997a) hypothesized non-monophyly of the family based on attributes of the nematocysts of some members of the family (e.g., *Daontesia*). Bathypheiliidae is distinguished by acontia containing a single type of nematocysts, and having macro- and micro-cnemes, an elongated body, and few tentacles.
- Boloceroiidae Carlgren, 1924** comprises three genera and approximately 10 valid species (Fautin 2007). Boloceroiidae belongs to infraorder Boloceroiaria, a small group distinguished by longitudinal muscles in the column, a disc-like aboral end, and the absence of basilar muscles. Boloceroiidae is distinguished from Nevadneidae, the other family of Boloceroiaria, in having an endodermal sphincter at the base of each tentacle.
- Capneidae Gosse, 1860** comprises two genera and five valid species (Carlgren 1949; Dunn 1982). Dunn (1983) reestablished and amended the name and authorship of the family, recognizing Aureliidae Andres, 1883 as a junior synonym. Capneidae is characterized by short, lobed tentacles that have a relatively unusual arrangement for actinarians: several tentacles arise from each principal endo- and exo-coel.
- Condylanthidae, Stephenson, 1922** comprises five genera and approximately 10 valid species (Fautin 2007). Members of this family have both macro- and micro-cnemes, a rare trait among actinarians with an endodermal sphincter.
- Diadumenidae Stephenson, 1920** is a monogeneric family comprising approximately 10 valid species (Fautin 2007). Members of Diadumenidae have two types of nematocysts in their acontia and lack a marginal sphincter; both of these attributes are seen in several other families.
- Edwardsiidae Andres, 1881** comprises seven genera and more than 100 valid species (Williams 1981; Daly 2002; Fautin 2007). Monophyly of Edwardsiidae has been demonstrated by analyses of molecular (Daly *et al.* 2002) and morphological (Daly 2002) data, and is evidenced by the shared, derived state of eight macrocnemes.

- Exocoelactiidae Carlgren, 1925** is a monogeneric family comprising two valid species from the deep sea (Arellano & Fautin 2001; Fautin 2007). Exocoelactiidae is characterized by a weak mesogleal sphincter and the irregular arrangement of the mesenteries in connection with the bilateral development of the younger mesenteries.
- Galatheanthemidae Carlgren, 1956** is a monogeneric family comprising two valid species restricted to abyssal-hadal depths (Fautin 2007). Galatheanthemidae is characterized by the formation of a chitinous tube that covers much of the animal's column, a strong mesogleal sphincter, and no basilar muscles.
- Gonactiniidae Carlgren, 1893** comprises two monospecific genera. Gonactiniidae belongs to a distinctive suborder of Actiniaria (Protantheae) distinguished by longitudinal muscles in the column, no ciliated tracts on the mesenterial filaments, no marginal sphincter, and no basilar muscles. In lacking all of these features, its members are unique among Actiniaria, and monophyly of the family is expected.
- Halcampidae Andres, 1883** comprises six genera and approximately 20 valid species (Fautin 2007). Halcampidae is characterized by an elongated body with cuticle, a marginal sphincter muscle that is either absent or mesogleal, and microcnemes. Because Halcampidae distinguished by absences rather than any uniquely present attributes, this family may not be monophyletic.
- Halcampoididae Appellöf, 1896** comprises eight genera and approximately 10 valid species (Dunn 1982; Fautin 2007). Halcampoididae is distinguished by no basilar muscles, a marginal sphincter, a variable number of mesenteries, and relatively longer tentacles in the inner cycle. Because none of these attributes are unique to this group, or even seen uniquely in combination in it, it is probable that Halcampoididae is not monophyletic. Furthermore, boundaries between Halcampoididae and Haloclavidae are not clearly established (Rodríguez & López-González 2003).
- Halcuriidae Carlgren, 1918** comprises two genera and approximately 10 valid species (Fautin 2007). Halcuriidae belongs to suborder Endocoelanthae, which is distinguished by an unusual arrangement of mesenteries; it is differentiated from all other members of the Endocoelanthae in having macro- and micro-cnemes and a unique siphonoglyph. The polarities of these diagnostic attributes are unclear, rendering assessment of its monophyly difficult.
- Haliactiidae Carlgren, 1949** comprises six genera and approximately 10 valid species (Fautin 2007). Haliactiidae is distinguished by an elongated body, microcnemes, acontia, and no basilar or marginal sphincter muscles. The absence of musculature that distinguishes Haliactiidae from Acontiophoridae may be a functional rather than a phylogenetic distinction (Hand 1961), and thus Haliactiidae may not be monophyletic.
- Haliplanellidae Hand, 1956** comprises two genera and two valid species (Dunn 1982; de Oliveira Pires 1987). Haliplanellidae is distinguished by the relatively small body size of its members, no marginal sphincter, and the types of nematocyst in the acontia. Because these attributes are all seen in other families, the monophyly of Haliplanellidae is unlikely.
- Haloclavidae Verrill, 1899** comprises eight genera and approximately 25 valid species (Rodríguez & López-González 2003; Fautin 2007). Haloclavidae is distinguished by a single well-developed siphonoglyph and no basilar muscles or marginal sphincter, rather than any unique attribute. The genera of Haloclavidae share relatively longer tentacles in the outer cycle and lack of basilar muscles, but are heterogeneous in terms of the column anatomy and the morphology of the sphincter muscle, which is either absent, weak and endodermal, or relatively strong and endodermal (Stephenson 1935, Carlgren 1949). The distinction between Haloclavidae and Halcampoididae is not clearly established (Rodríguez & López-González 2003). In phylogenetic analyses of molecular data (Berntson *et al.* 1999; Daly *et al.* 2003), the type genus *Haloclava* clusters with some members of Actiniidae.
- Hormathiidae Carlgren, 1932** comprises 15 genera and approximately 110 species, and is especially prominent in the deep sea (Fautin & Barber 1999; Fautin 2007). Some of its members occur symbiotically



with crustaceans or molluscs. Hormathiidae is characterized by having acontia containing only one type of nematocyst, a mesogleal marginal sphincter, and column divisible into two regions and usually provided with cuticle and tubercles.

**Iosactiidae Riemann-Zürneck, 1997** is a monogeneric family comprising one species from the deep-sea (Riemann-Zürneck 1997b; Fautin 2007). Iosactiidae is characterized by a burrowing habit, no basilar muscles, a small endodermal sphincter, 24 pairs of perfect mesenteries, and 24 deciduous tentacles, each with a sphincter. Its phylogenetic affinity is unclear: in having an endodermal sphincter and deciduous tentacles, it resembles some members of Actiniidae (e.g., *Bolocera*), but these same features, plus the number of mesenteries and general burrowing structure, relate it to Andresiidae.

**Isanthidae Carlgren, 1938** comprises five genera and seven valid species (Fautin 2007). Isanthidae is characterized by an elongated body, mesogleal marginal sphincter, and macro- and micro-cnemes.

**Isophelliidae Stephenson, 1935** comprises seven genera and approximately 35 valid species (Fautin 2007). Isophelliidae is distinguished by acontia containing two types of nematocysts and both macro- and micro-cnemes. Isophelliidae is very similar to Andvakiidae, differing only in the former having basilar muscles, although the two have traditionally been placed in separate superfamilies. Microcnemes, which are absent in Sagartiidae, are the sole attribute distinguishing Isophelliidae and Sagartiidae.

**Kadosactidae Riemann-Zürneck, 1991** comprises two genera and four valid species from the deep sea (Riemann-Zürneck 1991; Sanamyan & Sanamyan 2007). Kadosactidae is characterized by a column provided with cuticle and divisible into two regions, a strong mesogleal marginal sphincter, and acontia containing two types of nematocysts. The recent description of *Seepactis*, a second genus of Kadosactidae, renders the family heterogeneous.

**Limnactiniidae Carlgren, 1921** is a monogeneric family comprising two valid species (Fautin 2007). This family is characterized by no tentacles, marginal sphincter, or basilar muscles.

**Liponematidae Hertwig, 1882** is a monogeneric family comprising three valid species from deep-sea and polar waters (Fautin 2007). Liponematidae is characterized by attributes of its tentacles: each of the many tentacles has a sphincter at its base, allowing the tentacle to autotomize, and there is more than one tentacle per exocoel but only one per endocoel. Although its members resemble *Bolocera* (family Actiniidae) in general anatomy and cnidom, the arrangement of tentacles has been argued as sufficient to warrant family-level distinction (Dunn & Bakus 1977).

**Metridiidae Carlgren, 1893** comprises two genera and approximately five valid species (Fautin 2007). Metridiidae is distinguished in having acontia containing two types of nematocysts, a mesogleal marginal sphincter, and a lobed margin and oral disc with numerous short tentacles arrayed in the lobes. These attributes are not exclusive to members of Metridiidae.

**Minyadidae Milne-Edwards, 1857** comprises two genera and approximately five species (Fautin 2007). Its members are unique among Actiniaria in being neritic, using a chitinous float secreted by the pedal disc for buoyancy.

**Nemanthidae Carlgren, 1940** is a monogeneric family comprising three valid species (Fautin 2007). Nemanthidae is distinguished by acontia-like structures that are thicker than acontia but with fewer nematocysts that are not necessarily different than those of the filaments, and a mesogleal marginal sphincter.

**Nevadneidae Carlgren, 1925** is a monospecific family (Carlgren 1949; Fautin 2007). Nevadneidae belongs to Bolocerozoa, an infraorder of Actiniaria distinguished by the presence of longitudinal muscles in the column, a disc-like aboral end, and no basilar muscles. Nevadneidae it is differentiated from Bolocerozoa, the other family of Bolocerozoa, by an unusual arrangement of tentacles and in lacking a sphincter at the base of each tentacle.

**Octineonidae Fowler, 1894** is a monogeneric family with three valid species (Carlgren 1949; Fautin 2007). Octineonidae is acontiate, with a single type of nematocyst in the acontia, and thus resembles mem-

bers of the families Bathypheiliidae and Hormathiidae, from which it is distinguished by lacking basilar muscles.

**Oractiidae Riemann-Zürneck, 2000** is a monogeneric family comprising two valid species (Riemann-Zürneck 2000). Oractiidae is distinguished by an endodermal marginal sphincter, 10 pairs of mesenteries but only eight macrocnemes, one siphonoglyph, and no basilar muscles.

**Phymanthidae Andres, 1883** comprises two genera and approximately a dozen valid species (Fautin 2007). Phymanthidae is distinguished by verrucae on the distal column, a weak endodermal marginal sphincter muscle or none at all, and two kinds of tentacles: marginal ones arranged in cycles that may have knoblike or branched protuberances, and discal ones that are typically very short and arranged radially (Carlgren 1949).

**Preactiidae England in England & Robson, 1984** comprises two genera and two valid species (Fautin 2007). Its two species are very similar, sharing a suite of unusual attributes, including mesenteries of each pair fused medially at the animal's proximal end, and tentaculate vesicles on the column. Preactiidae is one of the two families comprising the former order Ptychodactiaria, currently included as a suborder within Actiniaria based on morphological data (Cappola & Fautin 2000; Fautin 2007). However, molecular evidence supports the inclusion of one of its species, *Dactylanthus antarcticus*, within the suborder Nynantheae, suggesting a close relationship with endomyarian actinarians (Berntson *et al.* 1999; Daly *et al.* 2003).

**Ptychodactiidae Appellöf, 1893** is a monogeneric family comprising one valid species (Fautin 2007). Ptychodactiidae is one of the two families comprising the former order Ptychodactiaria, currently included as suborder Ptychodacteae within Actiniaria based on morphological data (Cappola & Fautin 2000; Fautin 2007). However, morphological similarities with Preactiidae and the demonstrated close relationship between Preactiidae and members of the suborder Nynantheae suggest that Ptychodactiidae belongs among the endomyarian actinarians of suborder Nynantheae.

**Sagartiidae Gosse, 1858** comprises 14 genera and approximately 85 valid species (Carlgren 1949; Fautin 2007). Sagartiidae is characterized by a mesogleal marginal sphincter and acontia containing two types of nematocysts, attributes also seen in other families. The family is heterogeneous and is probably not monophyletic.

**Sagartiomorphidae Carlgren, 1934** is a monospecific family (Fautin 2007). Sagartiomorphidae is characterized by having a strong mesogleal marginal sphincter and acontia containing only one type of nematocyst. It differs from Hormathiidae in having microbasic amastigophores (referred to also as microbasic *p*-mastigophores) rather than basitrichs in the acontia, and from Sagartiidae in lacking basitrichs in the acontia.

**Stichodactylidae Andres, 1883** comprises two genera and approximately 10 valid species (Fautin 2007). Stichodactylidae is distinguished by a column typically bearing distal verrucae, a weak endodermal marginal sphincter, and short tentacles arranged in multiple endocoelic rows or long tentacles arranged in single endocoelic rows. Because of its distinctive arrangement of tentacles, this family has sometimes been accorded rank higher than family (e.g., Stephenson 1921).

**Thalassianthidae Milne-Edwards, 1857** comprises four genera and eight valid species (Fautin 2007). Thalassianthidae is distinguished by an oral disc typically lobed with endocoelic dendritic tentacles and nematospheres (globular tentacles with dense cnidae). The highly modified tentacles and their arrangement suggest monophyly of the family.

#### Order Antipatharia

S. C. France, M. Brugler & D. Opresko

The order Antipatharia Milne-Edwards & Haime, 1857 is composed of noncalcareous, colonial anthozoans characterized by a spiny, proteinaceous skeleton (corallum) that can be unbranched and wire-like or simply to

complexly dendritic. The skeleton is secreted by the axial epithelial tissue of the polyps in concentric layers around a small central hollow core. The polyps, each of which is often no more than a few millimeters in diameter (maximum size about 1 cm in diameter), possess six simple (unbranched) tentacles, six primary mesenteries, and zero, four, or six secondary mesenteries. The number of mesenteries and the morphology of the corallum, polyps, and axial spines are the principal taxonomic characters used in classification.

Antipatharians were originally grouped with gorgonians by Linnaeus, where they remained until Dana (1846) transferred them to the suborder Actinoidea. The Antipatharia was not recognized as a distinct order until the treatments of Milne-Edwards & Haime (1857) and Lacaze-Duthiers (1865). Prior to the 21<sup>st</sup> century and the work of Opresko (2001, 2002, 2003a, 2004, 2006), the last major taxonomic revision (van Pesch 1914) grouped all species into a single family, Antipathidae<sup>1</sup>. The current classification includes seven families, seven subfamilies, 40 genera, and 235 species; approximately a quarter of these have been described in the past two decades. Opresko (1972) provides an excellent history of the systematics and classification of antipatharians.

Black corals occur in all ocean basins, from 4,000 to 8,600 meters, although most species are found at depths >100 m (Grigg & Opresko 1977). Due to the relative inaccessibility of the deep-sea habitat, many species have been described from poor and incomplete material, including fragments of colonies, young colonies, or specimens without polyps. Characters used to distinguish antipatharian families include polyp structure (i.e., number of mesenteries, modification of the polyp shape, and possible differences in the absolute and relative size of the tentacles) and general morphology of the spines. Additionally, because the same corallum morphology may occur in different families, there may be uncertainties about family affinities if only the corallum, and not the soft tissue, is available for study. Missing type material and inadequate species descriptions have resulted in many species names that cannot be reliably identified, necessitating the establishment of neotypes. Over the past two decades there has been a spike in the number of new species descriptions (50 since 1990), largely as a result of technological breakthroughs allowing for increased sampling of deep-sea corals (Opresko 2005), and the revisionary works of Opresko (2001, 2002, 2003a, 2004, 2006), which have also erected 20 new genera and three new families since 2001.

Few published genetic studies have assessed phylogenetic relationships within Antipatharia, although several researchers are currently working on the group. Only a single study has examined the evolutionary relationships of select black coral families to one another, although the taxonomic and geographic coverage is very limited (15 species, representing seven genera and three families, all but one from Sulawesi (Indonesia); Lapian *et al.* 2007). Brugler and France (unpub. data) have analyzed three mitochondrial gene regions (two intergenic spacer regions and *cox1*) and the nuclear ITS region for species representing all families, and find strong support for monophyly of Cladopathidae, Leiopathidae, Myriopathidae, and Schizopathidae, as well as schizopathid subfamilies Parantipathinae and Schizopathinae. To date, we have sequenced an insufficient number of taxa to assess monophyly of the Stylopathidae, but our analyses suggest both Antipathidae and Aphanipathidae are polyphyletic and require further inspection. A preliminary cladistic analysis of morphological characters, with cerianthids (tube anemones) as the outgroup found the following associations (although many were polyphyletic): Schizopathidae was sister to Cladopathidae, a result strongly supported by DNA sequence analyses (Brugler & France unpub. data), Myriopathidae was sister to the Aphanipathidae, and Leiopathidae grouped with Antipathidae (Opresko, unpub. data).

#### *Included families*

**Antipathidae Ehrenberg, 1834** comprises five genera and approximately 100 species. The Antipathidae, the oldest and most species-rich family, is likely not monophyletic. It has historically been considered a

1. Except for *Dendrobrachia fallax* Brook, Family Dendrobrachiidae; this was later shown to be a misclassified octocoral (Opresko & Bayer 1991; Berntson *et al.* 2001).

taxonomic dumping ground and is thus, not surprisingly, morphologically heterogeneous, including polyps of variable size, skeletons of varying ramification, and spines of varying shape and size (e.g., Opresko & Baron-Szabo 2001; Opresko & Sanchez 2005). Several taxa have recently been transferred to new genera and families in the revisions of Opresko (2001, 2002, 2003a, 2004, 2006), and a revision of the remaining species is pending.

**Aphanipathidae Opresko, 2004** comprises nine genera and 22 species. Polyps have six primary and four secondary mesenteries, short, blunt, subequal tentacles, and spines that are tuberculate, but not notched, bifurcated or multiply-lobed at the apex. Two subfamilies (Aphanipathinae, Acanthopathinae) are differentiated by relative development of polypar spines. Phylogenetic analyses of DNA sequence data suggest the family is not monophyletic (Brugler & France, unpub. data).

**Cladopathidae Kinoshita, 1910** comprises six genera and 16 species (Opresko 2003a, 2005). The family is uniquely distinguished by the absence of secondary mesenteries. Polyps are transversely elongated with six primary mesenteries. The genera are further subdivided into three subfamilies: Cladopathinae, Hexapathinae, and Sibopathinae. The last is the only known anthozoan to lack an actinopharynx (and thus has only incomplete mesenteries). Morphological (Opresko, unpub. data) and molecular (Brugler & France unpub. data) phylogenetic analyses support monophyly of the family.

**Leiopathidae Haeckel, 1896** is a monogeneric family comprising six valid species, all of which are fairly distinctive from the remaining Antipatharia. Opresko (1998) suggested that the family may merit higher taxonomic status. Leiopathidae is distinguished by polyps with six primary and six secondary mesenteries, all of which are complete. The corallum is irregularly sympodial, with poorly developed spines and lacking pinnules.

**Myriopathidae Opresko, 2001** comprises five genera and 32 species. The family is distinguished by small polyps with short tentacles, six primary and four secondary mesenteries, distinct interpolypar spaces, and tall, conical spines on the corallum. Mitochondrial and nuclear sequences support monophyly of the family (Brugler & France, unpub. data).

**Schizopathidae Brook, 1889** comprises 11 genera and 37 species. Brook (1889) considered Schizopathidae to have 'dimorphic zooids' (two gonozooids flanking one gastrozoid, each bearing one pair of tentacles), but subsequent work has shown there is a single polyp type with lateral chambers specialized for reproduction (Opresko 2005). The family is distinguished by transverse elongation of polyps that have six primary and four secondary mesenteries. Genera are divided into two subfamilies that are differentiated by the transverse diameter of the polyp (Parantipathinae - 2-3 mm; Schizopathinae >3 mm). Molecular phylogenetic analyses provide good support for monophyly of the family and subfamilies (Brugler & France unpub. data).

**Stylopathidae Opresko, 2006** comprises three genera and nine species. The family is distinguished by the tendency of pinnules to occur in groups of two, three or four, and by parts of the corallum to fuse and anastomose. Spines are smooth, conical, and simple, with an acute or rounded apex. Polyps on the smallest branches are slightly elongated in the axial direction, but always smaller in diameter than those of the Schizopathidae.

#### Order Ceriantharia

M. Daly

The order Ceriantharia Perrier, 1883 comprises soft-bodied, solitary, elongate polyps with a ring of short labial tentacles in addition to the marginal tentacles. Ceriantharians have an arrangement of mesenteries unique among hexacorallians: mesenteries are coupled but not paired, with single mesenteries added only in the ventral intermesenterial compartment. Ceriantharians are burrowers, using their muscular column to penetrate sediment and producing a flexible, felt-like tube of discharged cnidae and mucus that sheaths the column.

Members of this order also possess a unique type of cnida, the ptychocyst, which is used in the construction of the tube (Mariscal *et al.* 1977). Because Ceriantharians have so many unique attributes, the group is inferred to be monophyletic, but no phylogenetic study has explicitly investigated this question.

Ceriantharia comprises approximately 100 named species, but diversity in this group remains poorly understood. Many species are known only from the long-lived, planktonic larval stage, the cerinula, and synonymies for even relatively common and well-known species are under active investigation (e.g., Molodtsova 2001a, 2001b, 2003; Wirtz *et al.* 2001). The number of genera is not clear: many monospecific genera have not been used since their creation, but have also not been formally synonymized. Dunn (1982) lists eight valid genera for the order, but Tiffon (1987) cites 18, and Fautin (2007) lists 39. The current higher-level classification was erected by den Hartog (1977), who used attributes of the cnidom to divide Ceriantharia into two suborders, Penicillaria and Spirularia. Penicillaria comprises only the family Arachnanthidae, and is characterized as having pencilli (also called microbasic *p*-mastigophores or microbasic amastigophores) (Schmidt 1972; den Hartog 1977). Spirularia comprises families Botrucnidiferidae and Cerianthidae, and lacks pencilli. The monophyly of each suborder and relationships within them remain unknown.

#### *Included families*

**Arachnanthidae McMurrich, 1910** is characterized by nematocyst-dense internal structures called acontioids. The family is composed of two genera known from adults and larvae, and several known from larvae only (Tiffon 1987).

**Botrucnidiferidae Carlgren, 1912** is characterized by nematocyst-dense internal structures called botrucnidae. The two most commonly encountered genera, *Botruanthus* and *Botrucnidifer*, are each known from a single species (Tiffon 1987).

**Cerianthidae Milne-Edwards & Haime, 1852** is characterized by lacking specialized nematocyst-bearing internal structure. It is composed of three genera known from both adults and larvae, and several genera known from larvae only (Tiffon 1987).

#### Order Corallimorpharia

M. Daly & D. G. Fautin

Members of order Corallimorpharia Carlgren, 1940 have had a complex taxonomic history that mirrors modern confusion about the phylogenetic position of this order within Hexacorallia. Corallimorpharians resemble actinarians in lacking a skeleton, and in being solitary or clonal rather than colonial. However, the internal morphology and cnidom of a corallimorpharian polyp is more similar to that of a scleractinian coral polyp (e.g., Gosse 1860; Moseley 1877; Schmidt 1972, 1974). In separating Corallimorpharia as a distinct order, Carlgren (1940) recognized that although they clearly have affinities with both actinarians and scleractinians, corallimorpharians are not easily accommodated in either group. The features used to identify Corallimorpharia are the same as those used for actinarians.

Molecular phylogenetic analyses have largely focused on the relationship between corallimorpharians and scleractinians. The results of these studies have been mixed: studies emphasizing DNA sequences from the mitochondrion or including a relatively sparse taxon sample (e.g., Fautin & Lowenstein 1994; Romano & Cairns 2001; Medina *et al.* 2006) typically recover Corallimorpharia nested within Scleractinia, whereas those that emphasize nuclear sequences or morphological data, or sample more broadly, find reciprocal monophyly of Scleractinia with respect to Corallimorpharia (e.g., Daly *et al.* 2003; Brugler & France 2007; Collins *et al.* 2006a; but see Chen *et al.* 1995). In nearly all analyses, Corallimorpharia is monophyletic, regardless of its relationship to Scleractinia. However, no analysis published to date has included multiple representatives of each putative lineage of Corallimorpharia, and thus monophyly is not established for any of its subordinal taxa. The chapter in this volume by Fautin *et al.* (2007) covers the genera of Actiniaria and Corallimorpharia.

### *Included families*

**Corallimorphidae Hertwig, 1882** comprises three genera and approximately 10 species (den Hartog 1980; Fautin 2007). Its members have retractile tentacles with acrospheres, and lack photosymbionts.

**Discosomatidae Duchassaing & Michelotti, 1864** comprises two genera and approximately 10 species (Dunn & Hamner 1980; den Hartog 1980; Fautin 2007). Its members have flat, disc-like polyps with discal and marginal tentacles. Discal tentacles are highly variable in morphology and are arranged in radial, endocoelic rows; marginal tentacles are typically small, often with acrospheres (Dunn & Hamner 1980; den Hartog, 1980). Carlgren (1949) erroneously used the junior synonym *Actinodiscus* instead of *Discosoma* in his influential classification and thus named the family Actinodiscidae; Doumenc and van Praët (1987) repeated this name in their treatment of the systematics of Corallimorpharia. Relationships among Discosomatidae have never been examined through phylogenetic analysis.

**Ricordeidae Watzl, 1922** is a monogeneric family comprising two valid species (den Hartog 1980; Fautin 2007). Its members have flat, disc-like polyps with short, simple tentacles arranged in radial, endocoelic rows. Neither the tentacles nor the oral disc are retractile. den Hartog (1980) proposed that Ricordeidae was intermediate between Corallimorphidae and Discosomatidae.

**Sideractiidae Danielssen, 1890** comprises two monospecific genera (Carlgren 1949; Doumenc & van Praët 1987; den Hartog *et al.* 1993). Its members are variable in column morphology, but all have tentacles with well-developed acrospheres that correspond in a one-to-one relationship with both the endocoelic and exocoelic spaces. The relationship between Sideractiidae and the other corallimorpharian families, which have multiple tentacles in each endo- and/or exo-coel, is unclear.

### Order Scleractinia

S. L. Romano & J. L. Stake

The Scleractinia Bourne, 1900 are polyp animals found exclusively in marine habitats. Its members are referred to as stony corals because all members of the order bear a solid calcareous skeleton that is external to the soft tissues, secreted by epidermal cells at the base of polyps to form cup-like calyces subdivided by septa and into which the polyp can retract for protection. Within the Anthozoa, such a skeleton is unique to the order. The approximately 1,300 described extant species (Cairns 1999) are divided ecologically into two main groups. One group, the reef builders, comprises 656 species. These are perhaps the best known scleractinian corals and are found mostly in the clear, shallow waters of the tropics. The second group, composed of 669 species, does not build reefs and is found in all regions of the oceans, including temperate and polar regions, and from relatively shallow waters to 6,000 m. The oldest scleractinian coral fossils are from the mid-Triassic (about 240 million years ago) and are similar to the scleractinians of today.

Higher-order relationships between families and suborders of scleractinians are poorly understood. The first comprehensive studies of scleractinian relationships in the mid-19<sup>th</sup> century were based on skeletal characters of both fossil and extant taxa (Milne-Edwards & Haime 1857; Ogilvie 1897). Vaughan and Wells' (1943) more recent treatment of the order revised several families, and is reflected in the current taxonomic organization of the order. The most widely accepted scleractinian phylogeny is that of Wells (1956), whose work is based on co-occurrence of genera in the fossil record and morphological characters of both fossil and extant scleractinians, but this phylogeny is not the product of an explicit phylogenetic analysis.

Scleractinian phylogeny has received renewed attention in recent years, primarily due to the availability of new techniques. Roniewicz and co-workers (Roniewicz & Morycowa 1993; Stolarski & Roniewicz 2001) used refined microstructural observations of both fossil and extant taxa to reevaluate scleractinian relationships. Veron (2000) has provided the most recent treatment of the order based on *in situ* observations and tra-

ditional morphological characters of extant taxa. However, his descriptions of new species bearing photosymbiotic dinoflagellates (= zooxanthellae) and revisions of families have not followed the International Code of Zoological Nomenclature, calling into question the taxonomic validity of his revisions. Phylogenetic analyses of molecular data have been used to reevaluate the relationships of families and genera within Scleractinia (Chen *et al.* 1995; Romano & Palumbi 1996; Veron *et al.* 1996; Romano & Cairns 2000; Cuif *et al.* 2003; Fukami *et al.* 2004; Le Goff-Vitry *et al.* 2004). Molecular characters are especially appealing as they are independent of morphological characters and the problems associated with them (determining homologies and high levels of variability). Formal revision of the order has not been proposed based on molecular phylogenetic studies despite development of new hypotheses for groupings within the order. Most recently, Kerr (2005) used a supertree approach based on matrix representation parsimony to provide a comprehensive hypothesis for relationships within the order based on both morphological and molecular data.

Wells (1956) divided the order into five suborders (comprising all fossil and extant taxa) but regarded hypothesized relationships among suborders as tentative, and made few hypotheses about relationships among families. Veron (1986, 1995, 2000) elevated some families to suborders, resulting in 24 extant families in seven suborders (with another six extinct suborders), but did not include any hypotheses for relationships among suborders due to poor understanding of skeletal homologies. Roniewicz and Morycowa's (1993) hypothesis for evolution within the Scleractinia is based primarily on fossil taxa with consideration of a small number of extant taxa. Their phylogeny is based on microstructural morphological characters and is very different from that of Wells (1956): it suggests that the order is polyphyletic, with the living families divided into two clades. Relationships of families within each of these clades are generally different from those of Wells' (1956) suborders. Phylogenetic analyses based on molecular data generally support traditional groupings of genera into families, but are not congruent with the limited hypotheses proposed for among family relationships. Molecular data suggests a split in the Scleractinia early in the evolutionary history of the group (Chen *et al.* 1995; Romano 1996; Veron *et al.* 1996; Romano & Cairns 2000; Chen *et al.* 2002; Cuif *et al.* 2003; Daly *et al.* 2003; Fukami *et al.* 2004; Le Goff-Vitry *et al.* 2004; Medina *et al.* 2006). The two clades supported by molecular data do not correspond to the two clades supported by microstructural morphological characters. Several families have member genera spread throughout the phylogenetic tree, with some appearing on opposite sides of the major scleractinian split. Romano and Palumbi's (1996) analysis suggest that this split occurred before the onset of the skeleton in Scleractinia, although further analyses by Medina *et al.* (2006) do not support this hypothesis. Debate about the origin of the scleractinian skeleton has further confounded the use of morphological characters for evaluating relationships within the order. Kerr's (2005) supertree analysis supports the division of the order into two major clades corresponding to those suggested by molecular data. This is not surprising given the predominance of molecular data in his analysis. The current state of taxonomy in the Scleractinia demonstrates the need for a comprehensive reevaluation of families and their relationships.

The following list of families still follows the nomenclature set forth by Wells (1956) with a few exceptions noted. For traditional family designations that are not supported by recent molecular studies, a brief description of the evidence is provided.

#### *Included families*

**Acroporidae Verrill 1902** comprises four genera, all zooxanthellate, and approximately 200 nominal species.

A phylogenetic analysis of the family was conducted as part of a monograph on the genus *Acropora* and found the family to be monophyletic (Wallace 1999). Subsequent analyses based on molecular data have found the family to be paraphyletic because the genus *Alveopora* (Poritidae) is found within the clade containing all of the acroporids (Fukami *et al.* 2000; Romano & Cairns 2000; Le Goff-Vitry *et al.* 2004; Kerr 2005).

**Agariciidae Gray, 1847** comprises six genera, all zooxanthellate, and approximately 45 nominal species. The family is considered to be monophyletic based on limited molecular data (Romano & Palumbi 1996;

Romano & Cairns 2000; Le Goff-Vitry *et al.* 2004; Kerr 2005). However, there has been no phylogenetic analysis of the entire family.

**Anthemiphylliidae Vaughan 1907** comprises a single genus with seven nominal species. All species are azooxanthellate. The family is considered monophyletic based on morphological and limited molecular data, although no phylogenetic analysis has been conducted on the family (Romano & Cairns 2000; Le Goff-Vitry *et al.* 2004; Kerr 2005).

**Astrocoeniidae Koby, 1890** currently comprises either two or four genera, depending upon the reference used (Wells 1956; Veron 2000). The family is polyphyletic, with one clade equal to *Madracis* sensu Veron (2000); Veron removed this genus from Pocilloporidae and placed it here. Molecular evidence does not support this move, and without *Madracis* the family is monophyletic according to limited molecular evidence (Romano & Cairns 2000; Le Goff-Vitry *et al.* 2004; Kerr 2005).

**Caryophylliidae Gray, 1846** comprises more than 50 genera and approximately 300 nominal species which are neither zooxanthellate or azooxanthellate. The subfamily Euphyllidae was elevated to family status by Veron (2000). Monophyly of the family is not supported by molecular phylogenetic analysis. The family is polyphyletic and molecular data suggests the family needs reevaluation (Romano & Cairns 2000; Le Goff-Vitry *et al.* 2004; Kerr 2005).

**Dendrophylliidae Gray, 1847** comprises 20 genera and approximately 150 nominal species. The majority of genera are azooxanthellate. A phylogenetic analysis by Cairns (2001) showed that the family is monophyletic. Limited molecular evidence also supports this conclusion (Romano & Cairns 2000; Cairns 2001; Le Goff-Vitry *et al.* 2004; Kerr 2005).

**Euphyllidae Veron, 2000** comprises five zooxanthellate genera and 14 nominal species. Veron (2000) elevated this subfamily of Caryophylliidae to family status because he found the designation of subfamilies to be artificial. The family has not been subject to phylogenetic analysis. The potential monophyly of the family remains in question and needs further evaluation.

**Faviidae Gregory, 1900** comprises 24 genera and over 100 nominal species that are all zooxanthellate. It is thought to be polyphyletic based on evidence in several molecular studies, although a complete phylogenetic analysis has not been conducted for the family (Romano & Cairns 2000; Cuif *et al.* 2003; Daly *et al.* 2003; Fukami *et al.* 2004; Le Goff-Vitry *et al.* 2004; Kerr 2005).

**Flabellidae Bourne, 1905** comprises 10 genera with approximately 100 nominal species, all of which are azooxanthellate. It is currently monophyletic based on morphological and limited molecular evidence, although no phylogenetic analysis has been conducted for the family (Cairns 1989; Romano & Cairns 2000; Le Goff-Vitry *et al.* 2004; Kerr 2005).

**Fungiacyathidae Chevalier, 1987** comprises one genus with approximately 20 nominal species, all of which are azooxanthellate. It is monophyletic based on morphological and limited molecular data (Cairns 1989; Romano & Cairns 2000; Le Goff-Vitry *et al.* 2004; Kerr 2005).

**Fungiidae Dana, 1846** comprises 11 genera with approximately 44 nominal species, all of which are zooxanthellate. It is considered monophyletic based on phylogenetic analysis of morphological data and limited molecular data (Cairns 1984a; Hoeksema 1989; Romano & Cairns 2000; Kerr 2005). Le Goff-Vitry *et al.* (2004) found weak support for paraphyly in the family with limited taxonomic sampling.

**Gardineriidae Stolarski, 1996** comprises a single genus made up of five nominal species, all of which are azooxanthellate. It is monophyletic based on morphological data but has not been the subject of a phylogenetic analysis (Stolarski 1996).

**Guyniidae Hickson, 1910** comprises seven genera with 10 nominal species. All genera are monospecific except *Guynia*. The family has been the subject of a phylogenetic analysis using morphological data (Stolarski 2000), but may be polyphyletic based on limited molecular data (Cuif *et al.* 2003; Le Goff-Vitry *et al.* 2004; Kerr 2005).



- Meandrinidae Gray, 1847** comprises seven genera after Veron (2000) placed three species from Caryophylliidae here. All of the genera are zooxanthellate. The genera within this family remain in question. There has not been a phylogenetic analysis conducted for the entire family. Fukami *et al.* (2004) found the family to be monophyletic with strong support; however, other molecular studies suggest the family is paraphyletic (Romano & Cairns 2000; Le Goff-Vitry *et al.* 2004; Kerr 2005).
- Merulinidae Verrill, 1866** comprises five genera with approximately 12 nominal species, all of which are zooxanthellate. The family is considered polyphyletic based on molecular evidence (Fukami *et al.* 2004; Kerr 2005); however, no complete phylogenetic analysis has been conducted for the family.
- Micrabaciidae Vaughan, 1905** comprises four genera with 13 nominal species, all of which are azooxanthellate. The family is monophyletic based on morphological data (Cairns 1989).
- Mussidae Ortmann, 1890** comprises 13 genera with almost 50 nominal species. All genera are zooxanthellate. The family is polyphyletic based on molecular data although the family has not been analyzed completely (Fukami *et al.* 2004; Kerr 2005).
- Oculinidae Gray, 1847** comprises 11 genera with approximately 30 nominal species. The family is split almost evenly between azooxanthellate and zooxanthellate genera. It is polyphyletic based on molecular evidence although no complete treatment of the family has been conducted (Romano & Cairns 2000; Le Goff-Vitry *et al.* 2004; Kerr 2005).
- Pectiniidae Vaughan & Wells, 1943** comprises five genera with almost 20 nominal species, all of which are zooxanthellate. Although the entire family has not been the subject of a phylogenetic analysis, it is considered polyphyletic based on limited molecular data (Fukami *et al.* 2004; Kerr 2005).
- Pocilloporidae Gray, 1842** comprises five genera, of which one is azooxanthellate, with over 30 nominal species. It has not been the subject of a phylogenetic analysis. Based on limited inclusion of some genera in the family, it is paraphyletic if *Madracis* is included (see Astrocoeniidae). With limited sampling and without *Madracis* the family forms a monophyletic clade based on molecular data (Romano & Cairns 2000; Cuif *et al.* 2003; Le Goff-Vitry *et al.* 2004; Kerr 2005).
- Poritidae Gray, 1842** comprises five genera containing over 70 nominal species, all of which are zooxanthellate. Although it has not been the explicit focus of any phylogenetic analysis, Poritidae is considered polyphyletic based on molecular evidence. The genus *Alveopora* is consistently found with the acroporids (Romano & Cairns 2000; Le Goff-Vitry *et al.* 2004; Kerr 2005).
- Rhizangiidae D'Orbigny, 1851** comprises five genera with more than 30 nominal species. All but one genus is azooxanthellate. The family is thought to be monophyletic, but there is little data available to confirm or refute this assertion (Kerr 2005).
- Siderastreidae Vaughan & Wells, 1943** comprises six genera with 27 nominal species, all of which are zooxanthellate. It has not been the subject of a phylogenetic analysis, but is considered polyphyletic based on molecular evidence from several representatives of the family used in larger analyses (Chen *et al.* 2000; Romano & Cairns 2000; Daly *et al.* 2003; Le Goff-Vitry *et al.* 2004; Kerr 2005).
- Trachyphylliidae Verrill, 1901** comprises a single zooxanthellate genus and a single species. The family is by definition monophyletic (Fukami *et al.* 2004; Kerr 2005).
- Turbinoliidae Milne-Edwards & Haime, 1848** comprises 22 genera and 51 nominal species, all of which are azooxanthellate. It is monophyletic based on morphological data (Cairns 1997; Kerr 2005).

#### Order Zoanthidea

M. Daly

Members of order Zoanthidea (= Zoantharia, Zoanthinaria) are clonal, soft bodied polyps with two rows of marginal tentacles. Their internal anatomy and mesenterial arrangement is distinctive among hexacorallians, and the group is presumed to be monophyletic, although no published studies have examined this question

explicitly. Less clear is the relationship between Zoanthidea and other members of Hexacorallia: this group has been interpreted as the sister group to Actiniaria (e.g. Schmidt 1974; Medina *et al.* 2006; Brugler & France 2007; Sinniger *et al.* 2007), as the basal member of a clade that also comprises Antipatharia, Corallimorpharia, and Scleractinia (Daly *et al.* 2003), and as the sister to Actiniaria, Antipatharia, Corallimorpharia, and Scleractinia (Brugler & France 2007). None of these analyses have considered many zoanthidean taxa, relative to the sampling for other lineages.

Zoanthideans have traditionally been grouped into two suborders: Macrocnemina and Brachycnemina, which differ in the arrangement of the mesenteries (Haddon & Shackleton 1891). Many Brachycnemina share a planktonic larval form (Ryland 1997; Ryland *et al.* 2000). Although these distinctions are well accepted and relatively clear, they seem not to reflect phylogenetic history. In their analysis of relationships among zoanthideans using mitochondrial DNA sequences, Sinniger *et al.* (2005) found that Macrocnemina is paraphyletic with respect to a monophyletic Brachycnemina. The results of Sinniger *et al.* (2005) highlight taxonomic difficulties in Zoanthidea, demonstrating para- and poly-phyly of many genera and families. Furthermore, studies of DNA sequences and of allozymes have indicated that there is significant cryptic diversity in Zoanthidea, suggesting that extensive revision of species and genera are necessary (Burnett *et al.* 1997; Ryland & Lancaster 2003; Sinniger *et al.* 2005; Reimer *et al.* 2006, 2007a, b). Because of this confusion at lower taxonomic levels, estimates of diversity should be considered tentative.

#### *Included families*

**Abysoanthidae Reimer & Fugiwara, 2007** in Reimer *et al.* 2007 is a monospecific family. This taxon was erected based on differences in DNA sequence and has not been characterized morphologically. Sequences of 16S rDNA and cytochrome oxidase subunit I from its sole species, *Abysoanthus nankaiensis*, were highly divergent compared to other zoanthideans. Phylogenetically, it is the basal-most member of the clade containing Epizoanthidae and Sphenopidae (Reimer *et al.* 2007a).

**Epizoanthidae Delage & Hirouard, 1910** comprises three genera and approximately five named species. Phylogenetic analysis of multiple representatives of three of its genera failed to recover its members as monophyletic; these taxa formed a paraphyletic grade with respect to Sphenopidae (Sinniger *et al.* 2005).

**Neozoanthidae Herberts, 1972** is a monogeneric family whose sole species has never been included in a phylogenetic analysis. The name has not been used by many other workers, and its species have not been reported since its description.

**Sphenopidae Hertwig, 1882** comprises three genera. The number of species in this group is unclear, in part because diversity of its two larger genera, *Palythoa* and *Protopalythoa* is poorly known (e.g. Burnett *et al.* 1997; Reimer *et al.* 2006, 2007b). Nonetheless, phylogenetic analysis of molecular sequence data from two species (in two genera) supported monophyly of the family (Sinniger *et al.* 2005).

**Zoanthidae Gray, 1840** comprises three genera and approximately five named species. Phylogenetic analysis of multiple representatives of three of its genera failed to recover its members as monophyletic; these taxa formed a paraphyletic grade with respect to Sphenopidae (Sinniger *et al.* 2005).

#### SUBCLASS OCTOCORALLIA

C. S. McFadden

The anthozoan subclass Octocorallia comprises the soft corals, gorgonians (sea fans, sea whips), sea pens, and blue coral. Octocorallia is currently estimated to include approximately 3,000 extant species. As the name suggests, the diagnostic apomorphies of the subclass are the eight tentacles and eight mesenteries of octocoral polyps, characters that are invariant within the clade. The presence of pinnules (lateral extensions) on the tentacles is also considered diagnostic, although this character is absent in several taxa (Alderslade & McFadden

2007). With only the single, well-documented exception of *Taiaroa tauhou*, all octocorals have colonial polyps. Because of the uniformity of polyp morphology across the group, Octocorallia has long been considered to be monophyletic (e.g., Dana 1846; Haeckel 1866; Kükenthal 1925), a conclusion that has been supported strongly by all molecular phylogenetic analyses of Anthozoa conducted to date (16S rDNA: France *et al.* 1996; 18S rDNA: Song & Won 1997; Berntson *et al.* 1999, 2001; Won *et al.* 2001; 28S rDNA: Chen *et al.* 1995).

Interpretations of relationships within Octocorallia vary widely, and at present there is little consensus among octocoral taxonomists about higher order relationships within the clade (Fabricius & Alderslade 2001; McFadden *et al.* 2006a). The sea pens (Pennatulacea) and blue corals (Helioporacea) have, however, been assigned to separate orders since the early 20<sup>th</sup> century (e.g., Hickson 1906; for a notable exception, see Kükenthal 1925). The unique colony form of sea pens, in which an axial polyp differentiates into a proximal peduncle and a distal rachis, represents a morphological synapomorphy that clearly unites order Pennatulacea and distinguishes its members from all other octocorals (Hickson 1930; Bayer 1956, 1981; Williams 1995, 1997). Likewise, Helioporacea, represented only by the monospecific *Heliopora* and one other enigmatic genus (Bayer 1992), are the only octocorals that produce a skeleton of crystalline aragonite, a convergent feature shared with the hexacorallian order Scleractinia.

Classification of the majority of octocorals—the soft corals and gorgonians—into higher taxonomic levels remains problematic, and in the past they have variously been divided among as few as two (Kükenthal 1925) and as many as six (e.g., Madsen 1944) orders. Historically, the most widely accepted classification, reflected in most mid-late 20<sup>th</sup> century invertebrate biology texts (e.g. Hyman 1940; Barnes 1980; Brusca & Brusca 1990), was that of Hickson (1930), who divided the soft corals and gorgonians among four orders (Alcyonacea, Gorgonacea, Stolonifera, Telestacea) distinguished by colony growth form. Recognition that these groups grade into one another without clear morphological distinctions led Bayer (1981) to merge them into a single order, Alcyonacea, a decision that has been embraced by modern taxonomists (e.g., Fabricius & Alderslade 2001). This large and morphologically diverse order is not, however, defined by any synapomorphies.

For taxonomic convenience, Alcyonacea is often sub-divided into six sub-ordinal groups representing different grades of colony form and skeletal composition, but it is widely acknowledged that these groups do not reflect phylogenetic relationships (Fabricius & Alderslade 2001). Indeed, molecular phylogenetic analyses using 18S rDNA and mitochondrial protein-coding genes have not recovered any of the sub-ordinal groups of Alcyonacea as monophyletic (Berntson *et al.* 2001; McFadden *et al.* 2006a). In addition, the distinctions between orders Alcyonacea, Pennatulacea, and Helioporacea have not been well supported by molecular studies. The 18S phylogeny of Berntson *et al.* (2001) found Pennatulacea to be polyphyletic; in contrast, McFadden *et al.*'s (2006a) mitochondrial gene phylogeny recovered a monophyletic Pennatulacea, but found it to be nested within a paraphyletic group of alcyonaceans as the sister clade to the gorgonian family Ellisellidae. The phylogenetic position of *Heliopora* with respect to the other octocorals remains unresolved (Berntson *et al.* 2001; McFadden *et al.* 2006a). Even though the traditional ordinal classification has not been well supported, most molecular phylogenetic studies conducted to date have nonetheless divided Octocorallia into two or three genetically distinct clades; morphological synapomorphies distinguishing these clades have, however, yet to be identified (Berntson *et al.* 2001; Sánchez *et al.* 2003a; McFadden *et al.* 2006a).

### Order Alcyonacea

As currently defined, order Alcyonacea Lamouroux, 1816 includes 30 families of soft corals (octocorals without a supporting skeletal axis) and gorgonians (octocorals with a supporting skeletal axis of scleroproteinous gorgonin and/or calcite) (Bayer 1981). Alcyonacean families are distinguished primarily on the basis of overall colony growth form, presence or absence of a supporting skeletal axis, and details of axial composition. The form and distribution of sclerites (microscopic calcite crystals embedded in the coenenchymal tissue and

polyps) are the most important characters used to distinguish genera and species of octocorals, but are less important for familial distinctions. Alcyonaceans are found worldwide, at all depths and in all oceans.

Within this large order, two groups of gorgonians, Calcaxonia and Holaxonia, are currently recognized as morphologically distinct suborders defined by skeletal apomorphies (Grasshoff 1999). An additional four “subordinal groups” (Alcyoniina, Protoalcyonaria, Scleraxonia, Stolonifera) are distinguished for convenience, but are recognized as grades of colony architecture rather than clades (Fabricius & Alderslade 2001). Molecular phylogenetic analyses unite the calcaxonian families in a clade with order Pennatulacea, with respect to which they are paraphyletic (McFadden *et al.* 2006a). The remaining alcyonaceans belong to one or more separate clades within which sub-ordinal and family relationships remain unresolved (Berntson *et al.* 2001; McFadden *et al.* 2006a). Many families and genera of Alcyonacea require extensive taxonomic revision, and numerous species remain either undescribed or simply unidentifiable; lost type specimens and the poor quality of most 19<sup>th</sup> and early 20<sup>th</sup> century species descriptions preclude species-level identifications in many groups (e.g., McFadden *et al.* 2006b). Estimates of numbers of species per family are consequently only rough approximations that may not accurately reflect actual numbers of valid species.

[**Group Alcyoniina:** colonies with polyps united within a fleshy mass of coenenchyme]

#### *Included families*

**Alcyoniidae Lamouroux, 1812** comprises 34 genera and approximately 430 species of fleshy or membranous soft corals with polyps not arranged in clusters. The family is defined by the absence of those characters that distinguish the other families belonging to group Alcyoniina, and, not surprisingly, molecular phylogenetic analyses indicate that it is not monophyletic (McFadden *et al.* 2006a).

**Nephtheidae Gray, 1862** comprises 20 genera and approximately 500 described species of soft corals (250 species in the genus *Dendronephthya* alone) that form upright, branched colonies with a distinct stalk, and usually have the polyps arranged in clusters along or at the ends of branches. Several genera, however, have digitate or lobate growth forms similar to those found in family Alcyoniidae. The family is not monophyletic (McFadden *et al.* 2006a).

**Nidaliidae Gray, 1869** comprises seven genera and approximately 75 species with an unbranched (digiform or capitata) or arborescent growth form. Colonies are typically stiff and brittle as a result of large, densely packed sclerites that are arranged longitudinally in the tissue surrounding the polyp cavities. The family is probably not monophyletic (McFadden *et al.* 2006a).

**Paralcyoniidae Bayer, 1981** comprises four genera and approximately 10 species of soft corals in which the entire polyparium is retractable into a capsule-like base. The genera *Paralcyonium*, *Studeriotus* and *Ceeceenus* appear to form a monophyletic group (McFadden *et al.* 2006a; McFadden, unpub. data), but a fourth monospecific genus (*Maasella*) has never been included in a phylogenetic analysis.

**Xeniidae Wright & Studer, 1889** comprises 14 genera and approximately 130 species of soft corals that lack mesenterial filaments in all but the asulcal pair of mesenteries and have sclerites that are typically in the form of small, smooth-surfaced platelets or corpuscles. The family appears to be monophyletic, with the possible exception of the genus *Anthelia*, which differs in sclerite ultrastructure (Alderslade 2000) and does not group with other xeniid genera in some molecular analyses (McFadden *et al.* 2006a).

[**Suborder Calcaxonia:** gorgonians with an axis of gorgonin containing large amounts of non-scleritic calcite (as internodes or embedded in the gorgonin) and without a hollow, cross-chambered central core]

#### *Included families*

**Chrysogorgiidae Verrill, 1883** comprises 12 genera and approximately 90 species of gorgonians characterized by regular, geometric branching patterns and a highly calcified axis that typically exhibits a metallic sheen. The family has not been the subject of a phylogenetic analysis.

**Dendrobrachiidae Brook, 1889** comprises three species in the enigmatic genus *Dendrobrachia*, gorgonians with an axis that is entirely proteinaceous, has conspicuous ridges and spines, and lacks a hollow core. Based on these skeletal characters, *Dendrobrachia* was originally assigned to the hexacorallian order Antipatharia (Brook 1889; Thomson 1910). The presence of polyps with eight pinnate tentacles was recently confirmed from newly collected material, however, and the genus has subsequently been transferred to Octocorallia (Opresko & Bayer 1991). The phylogenetic relationship of *Dendrobrachia* to other octocoral families remains uncertain (Berntson *et al.* 2001), although it shares some morphological characters with Chrysogorgiidae (Opresko & Bayer 1991).

**Ellisellidae Gray, 1859** comprises 10 genera and approximately 100 species of gorgonians with a strongly calcified axis and sclerites in the characteristic form of dumbbells, clubs or double-ended spindles ornamented with hemi-spherical tubercles. The 10 genera fall into three groups; within each, generic distinctions are unclear and it has been proposed that most genera should be reduced to subgeneric standing (Bayer & Grasshoff 1994). Morphological apomorphies and molecular analyses support monophyly of the family (McFadden *et al.* 2006a).

**Ifalukellidae Bayer, 1955** comprises two genera and six species of gorgonians with a highly calcified axis and minute sclerites with coarse surface texture, similar in form to those of Xeniidae. A molecular phylogenetic analysis of the mitochondrial *msh1* gene suggests the family is monophyletic (McFadden *et al.* 2006a).

**Isididae Lamouroux, 1812** comprises 38 genera and approximately 135 species of gorgonians divided among four sub-families. The family is distinguished by a segmented axis consisting of nodes of pure gorgonin alternating with solid (or occasionally tubular) non-scleritic calcareous internodes. The family has not been the subject of a phylogenetic analysis, but France and Brugler (unpub. data) have identified a mitochondrial genome arrangement synapomorphy for the subfamily Keratoisidinae.

**Primnoidae Gray, 1857** comprises 32 genera and approximately 210 species of gorgonians with a highly calcified axis and non-retractile polyps that are heavily armored with calcareous scales. The family has not been the subject of a phylogenetic analysis.

[**Suborder Holaxonia:** gorgonians with an axis consisting primarily of gorgonin, often with small amounts of embedded non-scleritic calcite, and with a hollow, cross-chambered central core]

#### *Included families*

**Acanthogorgiidae Gray, 1859** comprises six genera and approximately 110 species of gorgonians with conspicuous, non-retractile polyps and an axis of gorgonin surrounding a wide, hollow, cross-chambered central core. The family is not monophyletic, and several genera (*Acanthogorgia*, *Anthogorgia*) appear to be paraphyletic with Plexauridae (McFadden *et al.* 2006a).

**Gorgoniidae Lamouroux, 1812** comprises 17 genera and approximately 260 species of gorgonians with retractile polyps and an axis of gorgonin surrounding a narrow, hollow, cross-chambered central core. Several molecular phylogenetic analyses suggest the family is not monophyletic (Sánchez *et al.* 2003b; Wirshing *et al.* 2005; McFadden *et al.* 2006a).

**Keroeididae Kinoshita, 1910** comprises five genera and approximately 13 species of gorgonians with an axis of partially fused sclerites surrounding a hollow, cross-chambered central core. The family has not been the subject of a phylogenetic analysis.

**Plexauridae Gray, 1859** comprises approximately 38 genera and 365 species of gorgonians divided among two sub-families (Plexaurinae, Stenogorgiinae (=Paramuriceinae)) that have been treated as separate families by some authors (e.g., Bayer 1956). The family is distinguished by an axis with a wide, hollow, cross-chambered central core surrounded by gorgonin with locules (hollow spaces) that often contain embedded non-scleritic calcite; polyps are retractile. Plexauridae is not monophyletic: several

molecular phylogenetic studies have supported the separation of the two sub-families and identified several other distinct clades that are paraphyletic with respect to Acanthogorgiidae and Gorgoniidae (Sánchez *et al.* 2003b; Wirshing *et al.* 2005; McFadden *et al.* 2006a).

[**Group Protoalcyonaria:** solitary polyps]

*Included families*

**Haimeidae Wright, 1865** comprises four monospecific genera of solitary polyps. The validity of these genera and of the family itself is questionable. The family was dropped by Hickson (1930), but re-established by Bayer and Muzik (1976) following the discovery of the solitary polyp *Taiaroa*. Bayer (1981) did not, however, include Haimeidae in his classification.

**Taiaroidae Bayer & Muzik, 1976** is a monospecific family comprising the species *Taiaroa tauhou*. This species consists of solitary polyps, a growth form that distinguishes it from all other octocorals. Its phylogenetic position within Octocorallia remains unresolved (Berntson *et al.* 2001).

[**Group Scleraxonia:** colonies with an axis or internal axial-like layer composed predominantly of sclerites that may be either unfused or fused with calcite]

*Included families*

**Anthothelidae Broch, 1916** comprises approximately 13 genera and 55 species, often divided among three subfamilies. This family is distinguished by a medulla (inner tissue layer) that contains unfused sclerites and is separated from the cortex (outer tissue layer that houses the polyps) by longitudinal boundary canals. Inclusion of several anthothelid genera in molecular phylogenetic analyses of Octocorallia suggests the family is not monophyletic (McFadden *et al.* 2006a).

**Briareidae Gray, 1859** comprises two or three genera and approximately 10 species in which the medulla contains unfused sclerites and is not separated from the cortex by a ring of boundary canals. The family has not been the subject of phylogenetic analyses.

**Coralliidae Lamouroux, 1812** comprises three genera, one of them of uncertain status, and approximately 30 species of gorgonians with dimorphic polyps and an axis composed of sclerites fused together solidly with calcite. The family has not been the subject of a phylogenetic analysis.

**Melithaeidae Gray, 1870** comprises approximately six genera and 105 species of gorgonians with an axial medulla that consists of flexible nodes (free sclerites embedded in gorgonin) alternating with rigid internodes (sclerites fused with calcite). The five genera in sub-family Melithaeinae grade into one another morphologically and consequently have been collapsed into one to three genera by some authors (Bayer 1981; Grasshoff 1999; Ofwegen 1987; Fabricius & Alderslade 2001). The family has not been the subject of a phylogenetic analysis.

**Paragorgiidae Kükenthal, 1916** comprises two genera and 17 species of gorgonians with dimorphic polyps and an axial medulla formed by unfused sclerites. A recent cladistic analysis suggests the family is monophyletic (Sánchez 2005).

**Parisididae Aurivillius, 1931** is a monogeneric family of approximately five species of gorgonians having an axis of flexible nodes (free sclerites embedded in gorgonin) alternating with rigid internodes formed by tuberculate sclerites fused with calcite. The axis construction is similar to that of Melithaeidae, but the form of the sclerites in the nodes and internodes differs. The family has not been the subject of a phylogenetic analysis.

**Subergorgiidae Gray, 1859** comprises three genera and approximately six species of gorgonians with an axial medulla of partially fused sclerites that is separated from the cortex by a ring of longitudinal boundary canals. The family has not been the subject of a phylogenetic analysis.

[**Group Stolonifera:** colonies with polyps united basally by stolons that may fuse to form ribbons or thin membranes]

#### *Included families*

**Acrossotidae Bourne, 1914** is a monogeneric family comprising one or two species in the genus *Acrossota*.

The family is distinguished by the complete absence of pinnules on the tentacles, a trait that may, however, be shared by some species in other families (Alderslade & McFadden 2007). *Acrossota* has never been included in a phylogenetic analysis.

**Clavulariidae Hickson, 1894** comprises approximately 24 genera and 60 species, often divided among four sub-families. Species in this family are united only by their colony growth form, which consists of polyps that are connected basally by stolons or thin membranes. Although Clavulariidae has not been the subject of a phylogenetic analysis, the inclusion of several genera in broader analyses of sub-class Octocorallia suggests that the family is not monophyletic (McFadden *et al.* 2006a).

**Coelogorgiidae Bourne, 1900** is a monospecific family comprising the species *Coelogorgia palmosa*. This species forms colonies in which an elongated axial polyp buds daughter axial polyps that in turn produce short lateral polyps. Several molecular phylogenetic analyses support a sister relationship between this species and family Xenidae (McFadden *et al.* 2006a; McFadden *et al.*, unpub. data).

**Cornulariidae Dana, 1846** is a monogeneric family comprising approximately four species in the genus *Cornularia*. The family is distinguished by the presence of a chitinous outer sheath that forms a theca-like cup around the polyp. *Cornularia* has never been included in a phylogenetic analysis.

**Pseudogorgiidae Utinomi & Harada, 1973** is a monospecific family comprising the species *Pseudogorgia godeffroyi*. This species, in which a single, very long axial polyp differentiates into a blade-like colony with short lateral polyps embedded in its thick coenenchymal walls, is poorly known and has never been included in a phylogenetic analysis.

**Tubiporidae Ehrenberg, 1828** is a monogeneric family in which polyps are housed in vertical, calcareous tubes connected to one another by horizontal, stolonial platforms. *Tubipora musica* is well known, but the validity of several other nominal species is uncertain. A molecular phylogenetic analysis based on mitochondrial genes suggests a close relationship between *Tubipora* and some genera of Clavulariidae (McFadden *et al.* 2006a).

#### Order Helioporacea

The order Helioporacea Bock, 1938 comprises just two monogeneric families that are unique among octocorals in producing calcified skeletons of crystalline aragonite. The well-known blue coral, *Heliopora coerulea*, is distributed widely throughout the Indo-Pacific where it is a common member of shallow coral reef communities. The enigmatic genus *Epiphaxum* is known from only a few localities at depths of 50–400 m (Bayer 1992). The phylogenetic relationship of these two families to one another and to other Octocorallia remains uncertain.

#### *Included families*

**Helioporidae Moseley, 1876** is a monospecific family comprising the species *Heliopora coerulea*, the only octocoral known to produce a massive aragonite skeleton similar to that of Scleractinia. Polyps are housed within cylindrical tubes in the skeleton, and are interconnected via solenia; a thin layer of tissue containing solenia also covers the outer surface of the skeleton (Fabricius & Alderslade 2001).

**Lithotelestidae Bayer & Muzik, 1977** is represented by three extant and one fossil species of the genus *Epiphaxum* (Bayer 1992). This family has a stoloniferous growth form in which the stolons and the polyp calyces become calcified with non-scleritic aragonite.

## Order Pennatulacea

The sea pens, order Pennatulacea Verrill, 1865, are arguably the most morphologically distinctive group of octocorals, and achieve the highest level of colony integration among Anthozoa. Colonies develop from an axial polyp (oozoid) that differentiates into a bulbous peduncle used to anchor the colony in soft substrate, and a distal rachis that bears secondary polyps. The colony is usually supported by an internal, rod-like axis of non-scleritic calcite, similar in crystalline structure to that of the ellisellid gorgonians (Bayer 1955). The secondary polyps of sea pens are usually dimorphic, consisting of tentaculate autozooids and siphonozooids that lack or have greatly reduced tentacles (Williams 1995). The 14 families of Pennatulacea currently considered valid (Williams 1995) are distinguished largely by the arrangement of the secondary polyps around the rachis, with some families displaying distinctly bilateral colony symmetry. Sea pens live partially buried in soft sediments; although they reach their highest diversity in the deep-sea some species are found in shallow water, including Indo-Pacific coral reefs (Williams 1993) and estuaries (Imahara & Ogawa 2006).

Cladistic analyses of Pennatulacea using family-level morphological characters support the monophyly of the order (Williams 1993, 1997), as does a recent molecular phylogeny of Octocorallia based on several mitochondrial genes (McFadden *et al.* 2006a). No studies to date, however, have examined phylogenetic relationships among or within any families of sea pens. Although representatives of a number of genera have been included in recent molecular phylogenies (Berntson *et al.* 2001; McFadden *et al.* 2006a), taxon sampling is still too sparse to draw conclusions regarding monophyly of families. Most families are diagnosed by combinations of character states that are shared with other families, and relatively few families are distinguished by autapomorphies. The most recent taxonomic synopsis of Pennatulacea, summarized below, is that of Williams (1995); he emphasizes that many families are in need of taxonomic revision, and that estimates of numbers of valid species are consequently only approximate.

### *Included families*

**Anthoptilidae Kölliker, 1880** is a monogeneric family comprising at least two valid species of elongated, whip-like colonies with polyps that are arranged biserially, are non-retractile and lack calyces.

**Chunellidae Kükenthal, 1902** comprises three genera and approximately four species that have polyps arranged along the stalk in pairs or groups of three, separated from one another by bare rachis.

**Echinoptilidae Hubrecht, 1885** comprises two genera and seven described species of radially symmetrical colonies with non-retractile, bifurcated calyces.

**Funiculinidae Gray, 1870** is a monogeneric family comprising at least three species of whip-like colonies with polyps that are arranged biserially along the rachis and can retract into tubular, eight-toothed calyces.

**Halopteridae Williams, 1995** is a monogeneric family comprising at least six valid species of elongated, whip-like colonies with autozooids arranged in oblique rows (often forming raised ridges) along two longitudinal series.

**Kophobelemnidae Gray, 1860** comprises three genera and approximately 18 species of clavate colonies with polyps arranged biserially or along three sides of the rachis.

**Pennatulidae Ehrenberg, 1834** comprises six genera and approximately 50 species [sometimes separated into Pennatulidae (two genera) and Pteroeididae Kölliker 1870 (four genera)]. Colonies are bilaterally symmetrical with autozooids disposed along the margins of leaves that are in turn arranged laterally around the rachis.

**Protoptilidae Kölliker, 1872** comprises two genera and approximately seven species of bilaterally symmetrical colonies with retractile polyps that are arranged in one to three longitudinal series along the rachis.

**Renillidae Gray, 1870** is a monogeneric family comprising at least four species distinguished from other sea pens by their unique foliate colony growth form.



**Scleroptilidae Jungersen, 1904** is a monogeneric family comprising one valid species and several species of uncertain status. The polyps are arranged along the stalk in pairs or groups of three, separated from one another by bare rachis. This family is distinguished from Chunellidae by the presence of rod- or spindle-shaped sclerites in the rachis.

**Stachytilidae Kölliker, 1880** comprises two genera and four species of somewhat clavate, bilaterally symmetrical colonies with autozooids arranged biserially along the rachis in oblique rows.

**Umbellulidae Kölliker, 1880** is a monogeneric family comprising at least nine valid species of sea pens with a long, slender stalk and a single, terminal cluster of autozooids.

**Veretillidae Herklots, 1858** comprises five genera and approximately 35 species distinguished by radial symmetry of the colony and retractile autozooids without calyces.

**Virgulariidae Verrill, 1868** comprises five genera and approximately 40 species. Colonies are bilaterally symmetrical with autozooids disposed along the margins of leaves that are in turn arranged laterally around the rachis.

## CLASS CUBOZOA

A.G. Collins

Cubozoa is the most species-poor class of phylum Cnidaria, presently containing 36 valid species in two orders (Gershwin 2005a, 2005b, 2006a, 2006b). Linnaeus (1758) described the first cubozoan, *Carybdea marsupialis* (Linnaeus 1758). Given their distinctive features it is not surprising that as additional species were described, they were classified together (e.g., Gegenbaur 1856; Aggasiz 1862; Kramp 1961). Haeckel (1880) was the first to recognize them (in the taxon Cubomedusae) as distinct from other major groups of medusozoans. Werner (1973) elevated the group as class Cubozoa, after he and others recognized that the life cycle and polyps were quite distinct from those of Scyphozoa, in which cubozoan species had been classified.

Few tests of cubozoan monophyly have been conducted, but putative synapomorphies for the group can be found in the cladistic analyses of Schuchert (1993), Bridge *et al.* (1995), Marques and Collins (2004), and Van Iten *et al.* (2006). Cubomedusae are distinctive in exhibiting four perradial sensory rhopalia containing strikingly complex eyes with ocelli, vitreous bodies, lenses, and retinas (Pearse & Pearse 1978), as well as statocysts. A piece of tissue entirely of subumbrellar origin, known as the velarium, narrows the subumbrellar opening of cubozoans. The velarium is infused by canals and supported by perpendicularly arranged structures known as frenulae. The tentacles of cubomedusae are concentrated at the four interradial corners and have thickened muscular bases termed pedalia. Less readily observed diagnostic features of Cubozoa include the organization of the nervous system of the polyps and the process by which the solitary polyp entirely metamorphoses into a single juvenile medusa. Molecular analyses including approximately 10 cubozoan species have found robust support for cubozoan monophyly (Collins 2002; Collins *et al.* 2006a).

### Order Carybdeida

Four families are presently classified in Carybdeida Gegenbaur 1857 (see Gershwin 2005b, 2006b): Alatinidae, Carybdeidae, Tamoyidae, and Tripedaliidae. Species of Carybdeida can be recognized by their unbranched pedalia located at the four interradial corners of the bell margin. With the exception of one family, Tripedaliidae, pedalia and tentacles number four. Unlike most members of Chirodropida, species of Carybdeida lack gastric saccules. The only explicit tests of monophyly of the group were based on molecular data sampled from nine species representing three of the four families (Collins 2002; Collins *et al.* 2006a); the results strongly support monophyly of Carybdeida. Alatinidae is the only family not yet sampled, but it seems likely that the group has a single origin within Cubozoa.

### *Included families*

**Alatinidae Gershwin, 2005b** comprises two genera, one monospecific, the other with approximately 10 valid species (Gershwin 2005b). Its members have not been included in any phylogenetic analyses and its monophyly remains untested. Putative synapomorphies and distinguishing characteristics of alatinids are crescentic phacellae and T-shaped rhopalar niche ostia (Gershwin 2005b). Gershwin (2005b) noted that the cnidoms of Alatinidae and Tripedaliidae are similar.

**Carybdeidae Gegenbaur, 1857** is a monogeneric family with six valid species (Gershwin 2005b, 2006b; Gershwin & Alderslade 2005). Four of these have been sampled for molecular data (Collins 2002; Collins *et al.* 2006a). One of these species, *Carybdea sivickisi*, is clearly closely related to a representative of Tripedaliidae, a connection which has also been noted on morphological grounds (Gershwin 2006b). The other species of Carybdeidae can be distinguished by the presence of a heart-shaped opening of the rhopalar niche ostia.

**Tamoyidae Haeckel, 1880** comprises four genera and six valid species (Gershwin 2005a; Gershwin & Alderslade 2005). Two tamoyids representing two genera (one called 'Darwin carybdeid' has since been described as *Gerorgia rifkinae*, Gershwin & Alderslade 2005) have been sampled for molecular data and were found to form a well supported clade (Collins 2002; Collins *et al.* 2006a). Character variation across the different tamoyid genera is clearly laid out by Gershwin and Alderslade (2005), and the only character which appears to potentially be an unambiguous synapomorphy for the group should it prove to be monophyletic is the possession of frown-shaped rhopalar niche ostia (Gershwin 2005a).

**Tripedaliidae Conant, 1897** is a monogeneric family with two valid species (Moore 1988). Only a single species has been sampled for molecular data, and no explicit tests of the group's monophyly have been conducted. Species are easily distinguished from members of the other families of Carybdeida by the possession of multiple pedalia and tentacles (three for one species, two for the other) at the interradial corners of the bell margin.

### Order Chiropoda

Two families are currently classified in order Chiropoda Haeckel, 1880 (see Gershwin 2006a): Chiropsalmidae and Chiropidae. Members of Chiropoda are easily distinguished from those of the other cubozoan order Carybdeida by their branched pedalia bearing numerous tentacles. In addition, with the exception of one species, all chiropods possess gastric sacculs (often termed diverticula), a feature absent in Carybdeida. The only explicit tests of the monophyly of the order are weak in terms of taxon sampling, including one species from each order (Collins 2002; Collins *et al.* 2006a). Nonetheless, these found strong support for a clade of Chiropoda exclusive of Carybdeida.

### *Included families*

**Chiropidae Haeckel, 1880** comprises three genera with four valid species (Gershwin 2006a). Only a single species in this family has been sampled for molecular data (Collins *et al.* 2006a), and monophyly of the family has not been explicitly tested. It is unclear if any unambiguous putative synapomorphies exist for the group. Three species (in two genera) possess gastric sacculs that are branched, but the monospecific genus *Chiroadectes* lacks these structures altogether (Gershwin 2006a).

**Chiropsalmidae Thiel, 1936** comprises three genera and seven valid species (Gershwin 2006a). Only a single species in this family has been sampled for molecular data (Collins *et al.* 2006a), and monophyly of the family has not been explicitly tested. Chiropsalmids are distinguished from other chiropods by the presence of smooth, unbranched, finger-like gastric sacculs that lack any filaments.

## CLASS HYDROZOA

P. Cartwright & A.G. Collins

Hydrozoa comprises two reciprocally monophyletic clades, Trachylina and Hydroidolina (Collins 2002; Collins *et al.* 2006a), which together contain approximately 3,500 valid species (Schuchert 2007a). Molecular and morphological phylogenetic analyses robustly support monophyly of Hydrozoa (Bridge *et al.* 1992; Collins 2002; Marques & Collins 2004; Collins *et al.* 2006a). Despite wide consensus regarding the monophyly and composition of Hydrozoa, it has few unambiguous, diagnostic morphological apomorphies. The cladistic analyses of Schuchert (1993), Bridge *et al.* (1995), Marques and Collins (2004), and Van Iten *et al.* (2006) identify sets of putative synapomorphies for Hydrozoa. Gap junctions have only been documented in hydrozoans within Cnidaria. If medusae are present in the life cycle, they usually possess a velum and two nerve rings, and are budded laterally from the polyps rather than arising by strobilation, as in Scyphozoa, or by complete transformation of the polyp, as in Cubozoa. Hydrozoan polyps lack septae. Most hydrozoans have gametogenic tissue of ectodermal origin and location, in contrast with non-hydrozoan cnidarians, which possess gametogenic tissue of endodermal origin and location.

### SUBCLASS HYDROIDOLINA

Hydroidolina Collins, 2000 includes Anthoathecata, Leptothecata, and Siphonophorae (see Marques & Collins 2004; Collins *et al.* 2006a). The monophyly of Hydroidolina is well supported by phylogenetic analyses of molecular (Bridge *et al.* 1995; Collins 2002; Collins *et al.* 2006a) and morphological (Bouillon & Boero 2000a; Marques & Collins 2004) data. The statocysts of Hydroidolina, when present, are ectodermal in origin. Hydroidolina polyps may be solitary or colonial, and the colonies may be polymorphic, a state that is only present in one genus (*Monobrachium*) of Trachylina. The relationships between major groups of Hydroidolina (Leptothecata, Anthoathecata, Siphonophorae) are uncertain (Collins 2002; Collins *et al.* 2006a).

#### Order Anthoathecata

Anthoathecata Cornelius, 1992 comprises two suborders, Filifera and Capitata, and approximately 1,140 valid species (Bouillon *et al.* 2006). The polyps do not have a skeletal covering and can be solitary or colonial. The medusae do not have statocysts and the gametogenic tissue is confined to the manubrium. Molecular phylogenetic studies do not support monophyly of Anthoathecata, suggesting instead that Anthoathecata is a paraphyletic assemblage that gave rise to one or more of the other suborders of Hydroidolina (Collins *et al.* 2006a).

#### Suborder Filifera

Filifera comprises 22 families (Schuchert 2007a) and approximately 765 valid species (Bouillon *et al.* 2006). Although the suborder has the putative morphological synapomorphies of filiferan tentacles on the feeding polyps and desmoneme and eurytele nematocysts, molecular phylogenetic analyses do not support its monophyly (Collins 2002; Collins *et al.* 2005, 2006a).

#### *Included families*

**Australomedusidae Russell 1971** comprises three genera (Schuchert 2007a) and approximately five valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic anal-

yses and its members have never been the subject of a phylogenetic analysis. This family is distinguished by polyps with large extensible hypostomes and medusae with (usually) four radial canals and four clusters of tentacles at the perradii of the bell margin.

**Balellidae Stechow 1922** is a monospecific family (Bouillon *et al.* 2006) whose sole species has not been included in molecular phylogenetic analyses. This family is distinguished by polyps with two widely separated whorls of filiform tentacles.

**Bougainvilliidae Lütken, 1850** comprises 13 genera (Schuchert 2007a) and approximately 100 valid species (Bouillon *et al.* 2006). Bougainvilliidae includes *Rhizorhagium*, which is not found within Schuchert's (2007b) classification (2007a). Molecular phylogenetic analyses that include two species from two genera were ambiguous with regard to monophyly (Collins *et al.* 2006a) and the group awaits a thorough phylogenetic investigation. Bougainvilliidae lacks morphological synapomorphies and shares many features with other families (Calder 1988; Schuchert 2007c). Some genera classified elsewhere by Schuchert (2007a), e.g., *Lizzia* in Rathkeidae, have been considered part of Bougainvilliidae (Bouillon *et al.* 2006).

**Bythotiaridae Maas, 1905** comprises nine genera (Schuchert 2007a) and approximately 25 valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of a phylogenetic analysis. Hydroids from this family can be distinguished by their habit of living inside the prebranchial cavity of ascidians. Medusae are recognized by marginal tentacles that have tiny or absent basal bulbs and terminate in a cluster of cnidae, but these features are present in Eucodoniidae.

**Clathrozoellidae Peña Cantero, Vervoort & Watson, 2003** is a monogeneric family (Schuchert 2007a) with four valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses. This family is distinguished by a pseudohydrotheca covering the polyps.

**Cytaeididae Agassiz, 1862** comprises three genera (Schuchert 2007a) and approximately 20 valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. There are no known morphological synapomorphies for this group and the validity of one of the genera (*Perarella*) is questionable (Bouillon *et al.* 2006; Schuchert 2007c).

**Eucodoniidae Schuchert, 1996** is a monospecific family (Schuchert 1996) that has not been included in molecular phylogenetic analyses. This family is distinguished by four clusters of embedded nematocysts around the mouth margin of medusae (Schuchert 1996).

**Eudendriidae Agassiz, 1862** comprises two genera (Schuchert 2007a) and approximately 85 valid species (Marques 1996). Only a single representative has been included in molecular phylogenetic analyses (Collins *et al.* 2006a). Possible synapomorphies for this group include the absence of desmoneme nematocysts, a styloid gonophore, and trumpet-shaped hypostome (Marques 1996).

**Hydractiniidae Agassiz, 1862** comprises seven genera (Schuchert 2007a) and approximately 100 valid species (Bouillon *et al.* 2006). Eleven species representing two genera have been included in molecular phylogenetic analyses, which supported monophyly of the group (Cunningham & Buss 1993). However, taxon sampling in this analysis was not broad. The hydractiniid genus *Clava* is sometimes classified together with genera of Oceanidae in the family Clavidae (see Bouillon *et al.* 2006), suggesting that its phylogenetic status is uncertain. Hydroids of the family are distinguished by stolonial, polymorphic colonies that may bear spines.

**Laingiidae Bouillon, 1978** comprises three genera and four valid species (Bouillon 1978; Bouillon *et al.* 2006). One species has been included in molecular phylogenetic analyses (Collins *et al.* 2006a). This group was originally classified as its own subclass by Bouillon (1978) but molecular phylogenetic analyses have shown that at least one member of the group, *Fabienna sphaerica*, is nested within Hydroidolina and closely related to Proboscidactylidae (see Collins *et al.* 2006a). This hypothesis is

supported by morphological data, including a solid radial canal and macrobasic euryteles (Schuchert 1996).

**Niobiidae Peterson, 1979** is a monospecific family (Bouillon *et al.* 2006) whose sole species has not been included in molecular phylogenetic analyses. The hydroid stage is unknown and the medusae are distinguished by marginal tentacle bulbs that develop into medusae buds (Petersen 1979).

**Oceanidae Eschscholtz, 1829** comprises eight genera (Schuchert 2004) and approximately 25 valid species (Bouillon *et al.* 2006). Representatives of the family have not been included in any phylogenetic analyses. The family is distinguished by scattered filiform tentacles on the polyps, but this character is not specific to this group (Calder 1988; Schuchert 2004). Several genera of this family are sometimes classified with *Clava* in the family Clavidae (see Bouillon *et al.* 2006), suggesting that its phylogenetic status is uncertain.

**Pandeidae Haeckel, 1879** comprises 23 genera (Schuchert 2007a) and approximately 75 valid species (Bouillon *et al.* 2006). One species has been included in molecular phylogenetic analyses (Collins *et al.* 2006a), but no explicit analyses of its phylogeny have been attempted. There are no known synapomorphies for this group and it is probably not monophyletic, as it encompasses a diverse assemblage of genera (Calder 1988).

**Proboscidiactylidae Hand & Hendrickson, 1950** is a monogeneric family (Schuchert 2007a) with six valid species (Bouillon *et al.* 2006). One species has been included in molecular phylogenetic analyses (Collins *et al.* 2006a). Hydroids of this family are distinguished by polymorphic stolonal colonies bearing gastrozoid polyps with two filiform tentacles.

**Protiaridae Haeckel, 1879** comprises five genera (Schuchert 2007a) and approximately eight valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses. Medusae of this family are distinguished by large, hollow tentacular bulbs and four well-developed tentacles that are often interspersed with short, solid tentacles.

**Ptilocodiidae Coward, 1909** comprises six genera (Schuchert 2007a) and eight valid species (Bouillon *et al.* 2006). The group has not been the subject of a phylogenetic analysis. Hydroids of this family are distinguished by the absence of tentacles on the feeding polyps.

**Rathkeidae Russell, 1954** comprises six genera (Schuchert 2007a) and approximately 20 valid species (Bouillon *et al.* 2006). Three species representing three genera have been included in molecular phylogenetic analyses and in phylogenetic analyses, and these support familial monophyly (Schuchert 2007a). Species of this family are distinguished by primary medusae buds arising from stolons and secondary medusae buds arising interradially from the medusa manubrium.

**Rhysiidae Brinckmann, 1965** is a monogeneric family (Schuchert 2007a) with three valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses. This family is distinguished by dactylozooids covered with perisarc to the capitate apical tip and female gonozooids that transform into a sporosac-like structure.

**Russelliidae Kramp, 1957** is a monospecific family (Bouillon *et al.* 2006) whose sole species has not been included in molecular phylogenetic analyses. The hydroid stage is unknown and the medusa possesses marginal tentacles in groups of three: one large and two small hollow tentacles. The large tentacles are sunk into the umbrella margin, forming a furrow.

**Stylasteridae Gray, 1847** comprises 26 genera (Schuchert 2007a) and approximately 260 valid species (Bouillon *et al.* 2006). Cairns (1984b) published a cladistic analysis of the genera of this diverse group, but its monophyly was not tested because only one outgroup was considered. Nevertheless, species of the group are readily distinguished by a massive calcareous exoskeleton, often brightly pigmented, and they very likely form a clade.

**Trichyridae Hincks, 1868** is a monospecific family (Bouillon *et al.* 2006) whose sole species has not been included in molecular phylogenetic analyses. No putative synapomorphies are known in the hydroid stage, but medusae are distinguished by the possession of many tiny, anastomosing centripetal canals.

**Tubiclavoididae Moura, Cunha & Schuchert, 2007** is a monospecific family (Moura *et al.* 2007) whose sole species has been included in molecular phylogenetic analyses (Moura *et al.* 2007), the results of which have not been published. The species is characterized by elongate polyps with scattered filiform tentacles and hydrocauli covered with striated perisarc.

#### Suborder Capitata

Capitata comprises 26 families (Schuchert 2007a) and approximately 375 valid species (Bouillon *et al.* 2006). The putative synapomorphies are stenotele nematocysts and capitata tentacles on the polyps or filiform tentacles in separated whorls (Bouillon & Boero 2000b). Molecular phylogenetic analyses suggest that Capitata is a paraphyletic assemblage containing two clades, Aplanulata and the other capitates (Collins 2002; Collins *et al.* 2005, 2006a). The synapomorphy for Aplanulata is the absence of a ciliated planula larva (Petersen 1990). Four families, Tubulariidae, Corymorphidae, Candelabridae, and Hydridae have been sampled in molecular phylogenetic analyses that support monophyly of Aplanulata (Collins *et al.* 2005; Collins *et al.* 2006a), but it is likely that other families are part of this group (Petersen 1990; Collins *et al.* 2006a). Mosaics of features, very few of which appear to be unique to any particular family, distinguish the medusa stages of capitata families.

#### *Included families*

**Acaulidae Fraser, 1924** comprises three genera and five valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. Members of this family are distinguished by scattered capitata tentacles on the distal portions of their solitary polyps.

**Boeromedusidae Bouillon, 1985** is a monospecific family (Bouillon *et al.* 2006) whose sole species has not been included in molecular phylogenetic analyses. Hydroids are unknown; medusae have an apical projection, four tentacles terminating in nematocyst clusters, and four periradial pouches bearing gametes hanging from the manubrium.

**Boreohydridae Wesblad, 1947** comprises two genera (Bouillon 1985) and two valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. This family is distinguished by small solitary polyps that possess a whorl of three to five diminutive tentacles (Schuchert 2006).

**Candelabridae Stechow, 1921** comprises three genera (Schuchert 2006) and approximately 20 valid species (Bouillon *et al.* 2006). Just a single representative has been included in molecular phylogenetic analyses (Collins *et al.* 2005) and no explicit tests of the group's monophyly have been conducted. The family is distinguished by its solitary or pseudo-colonial polyps that are relatively large and bear numerous scattered capitata tentacles (Schuchert 2006).

**Cladocorynidae Allman, 1872** comprises two genera (Schuchert 2006) and seven valid species (Bouillon *et al.* 2006). Only a single representative has been included in molecular phylogenetic analyses (Collins *et al.* 2005) and no explicit tests of the group's monophyly have been conducted. The putative synapomorphy for the family is patches of macrobasic euryteles on the body wall of the polyp (Petersen 1990).

**Cladonematidae Gegenbaur, 1856** comprises four genera (Schuchert 2006) and approximately 20 valid species (Bouillon *et al.* 2006). Phylogenetic analyses including three species representing two genera support monophyly of the group (Collins *et al.* 2005). The family is distinguished by benthic medusae with branched tentacles and adhesive structures at the tips of the medusae tentacles (Petersen 1990).

- Corymorphidae Allman, 1872** comprises 10 genera (Schuchert 2007a) and approximately 45 valid species (Bouillon *et al.* 2006). Two species from one genus were included in molecular phylogenetic analyses, the results of which contradicted monophyly (Collins *et al.* 2005). There are no known synapomorphies for this group (Petersen 1990).
- Corynidae Johnston, 1836** comprises seven genera and approximately 90 valid species (Schuchert 2001). A molecular phylogenetic analysis sampling 13 species from four genera strongly contradicted monophyly of the group, with some species being closely allied to members of Polyorchidae (Collins *et al.* 2005). Not surprisingly, no morphological synapomorphies have been identified for Corynidae (Schuchert 2001).
- Halimedusidae Arai & Brinckmann-Voss, 1980** comprises three genera (Mills 2000; Schuchert 2007a), each with a single valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. Species of this family have small solitary polyps that give rise to medusae with distinct inter-radial peaks in jelly above the manubrium base, a feature also present in medusae of Boeromedusidae (Mills 2000).
- Hydridae Linnaeus, 1758** is a monogeneric family (Schuchert 2007a) with approximately 30 valid species (Bouillon *et al.* 2006). A molecular phylogenetic analysis sampling three species representing both the green and brown hydra groups supported monophyly of the family (Collins *et al.* 2006a). Hemmrich *et al.* (2007) sampled additional taxa (mainly focused on laboratory strains) and also found the group to be monophyletic, although this study aimed at elucidating relationships within the group. Hydridae is distinguished by the absence of medusae, its freshwater habitat, and lateral budding of polyps.
- Hydrocorynidae Rees, 1957** comprises two genera (Schuchert 2007a) and three valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. Hydroids of the group are colonial, with hydranths arising from a chitinized hydrorhizal plate. No putative synapomorphies have been identified for the medusa stage.
- Margelopsidae Uchida, 1927** comprises three genera (Schuchert 2006) and six valid species. No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. The family is distinguished by its small, pelagic, solitary polyps.
- Milleporidae Fleming, 1828** is a monogeneric family with approximately seven valid species (Razak & Hoeksema 2003). One species has been sampled for molecular analysis (Collins *et al.* 2006a). This family is distinguished by colonies that build massive calcareous skeletons, polyps with capitate tentacles, and dimorphism with gastrozooids and dactylozooids.
- Moerisiidae Poche, 1914** comprises three genera (Schuchert 2007a) and fewer than 10 valid species (Bouillon *et al.* 2006). One representative has been included in molecular phylogenetic analyses (Collins *et al.* 2005), but the family has never been the subject of an explicit phylogenetic analysis. Polyp stages of this family, where known, are solitary with scattered filiform tentacles. Medusae are recognized by a manubrium with radial lobes that extend toward and connect with the radial canals.
- Paracorynidae Picard, 1957** is a monospecific family (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses. This family is distinguished by a flat, highly organized colony, with polymorphic zooids. Bouillon (1974) suggested that *Paracoryne* could be interpreted as an individual flattened polyp, rather than as a colony.
- Pennariidae McCrady, 1859** is a monogeneric family with two valid species (Schuchert 2006). A single, widespread representative has been included in molecular phylogenetic analyses and no explicit tests of the group's monophyly have been conducted. The family is distinguished by a pinnate hydroid colony with polyps that contain an aboral whorl of filiform tentacles and capitate tentacles scattered

towards the oral end.

**Polyorchidae Agassiz, 1862** comprises three genera (Schuchert 2007a) and five valid species (Bouillon *et al.* 2006). Three species from two genera have been included in molecular phylogenetic analyses, which strongly supported monophyly of the group (Collins *et al.* 2005). The hydroid is unknown. Its large medusae are distinguished by a conspicuous gastric peduncle, a manubrium with four oral lips studied with nematocysts, numerous tentacles, and abaxial ocelli.

**Porpitidae Goldfuss, 1818** comprises two genera and three valid species (Kirkpatrick & Pugh 1984). One species from each genus was sampled in a molecular phylogenetic analysis, and the family was found to be monophyletic (Collins *et al.* 2005). This family is distinguished by a highly polymorphic, pelagic colonial stage, although it has been argued that this is not a colony but a modified individual polyp (Petersen 1990).

**Protohydridae Allman, 1888** is a monogeneric family with two valid species (Schuchert 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. The family is distinguished by small polyps that lack tentacles and gonophores and a pedal disk that is epidermal in origin (Petersen 1990).

**Solanderiidae Marshall, 1873** is a monogeneric family (Schuchert 1996) with approximately seven valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. Species of the family are easily recognized by their large, branching colonies with chitinous, anastomosing internal skeletons.

**Sphaerocorynidae Prévot, 1959** comprises two genera (Petersen 1990) and approximately five valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. Hydroids of the family are long-stemmed and scattered with capitate tentacles at the broadest part of the hydranth. Medusae possess apical projections with an apical chamber and a single abaxial ocellus on each of four tentacles; each tentacle terminates in an elliptical nematocyst pad.

**Teissieridae Bouillon, 1974** comprises three genera (Petersen 1990) and approximately 10 valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. Two genera are sometimes classified in a separate family (Bouillon *et al.* 2006). This family is distinguished by a colony with a unique basal plate of periderm that forms spines.

**Tricyclusidae Kramp, 1949** is a monospecific family (Schuchert 2006) whose sole member has not been included in molecular phylogenetic analyses. This family is distinguished by solitary polyps that have a gelatinous perisarc and three whorls of capitate tentacles.

**Tubulariidae Fleming, 1828** comprises six genera (Schuchert 2007a) and approximately 60 valid species (Bouillon *et al.* 2006). Four species from three different genera have been sampled in a molecular phylogenetic analysis and found to be monophyletic (Collins *et al.* 2005). Although no explicit test of the group's monophyly was conducted, a larger study subjected 32 species to morphological phylogenetic analyses (Marques & Migotto 2001). This study did support reciprocal monophyly of two subfamilies, Ectopleurinae and Tubulariinae. The family is distinguished by polyps possessing two sets of tentacles, an aboral and oral whorl with gonophores developing between the sets of tentacles. The medusae often have a manubrium surrounded by gametogenic tissue. Based on these features and the molecular data, monophyly of the family is likely.

**Zanleidae Russell, 1953** comprises four genera (Schuchert 2007a) and approximately 25 valid species (Bouillon *et al.* 2006). Two species from one genus have been included in molecular phylogenetic analyses (Collins *et al.* 2005), but no detailed analyses of the groups' phylogenetic status have been conducted. Phylogenetic analyses contradict monophyly, although the node separating these species



was poorly supported (Collins *et al.* 2005). Hydroids of the family possess no obvious putative synapomorphies. Zancleid medusae have four perradial exumbrellar nematocyst pads.

**Zancleopsidae Bouillon, 1978** comprises two genera (Petersen 1990) and six valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of an explicit phylogenetic analysis. The hydroid phase is unknown. Medusae have a conical or dome-shaped umbrella without an apical chamber, and usually have two opposed capitata tentacles that typically have capitata side branches.

### Order Leptothecata

Molecular and morphological phylogenetic analyses support monophyly of Leptothecata Cornelius, 1982 (e.g., Collins *et al.* 2006a; Leclère *et al.* 2007). The synapomorphy for Leptothecata is the theca, a skeletal covering on the polyps (hydrotheca) and gonophores (gonotheca). However, some phylogenetic analyses have identified a theca-less taxon as the earliest diverging lineage of Leptothecata, suggesting that the theca may have evolved after the origin of Leptothecata. Leptothecate polyps are always colonial and the tentacles of the polyps are arranged in a single whorl. The medusae usually have shallow bells with gametogenic tissue restricted to the radial canals. The approximately 2,000 valid species are classified into two suborders, Conica and Proboscidoidea (Bouillon *et al.* 2006). When families of Leptothecata are distinguished based on features of the medusa stage, suites of characters are typically used although very few individual characters are unique to any particular family.

#### Suborder Conica

Conica is the more diverse of the two orders of leptothecates, comprising approximately 1,770 valid species (Bouillon *et al.* 2006) in 29-31 families (Bouillon *et al.* 2006; Schuchert 2007a). The presumed synapomorphy of the suborder is a conical hypostome on the polyps. Leclère *et al.* (2007) did not recover a monophyletic Conica; however this work addressed a different question and support in the relevant part of the topologies was weak.

#### *Included families*

**Aequoreidae Eschscholtz, 1829** comprises four genera (Schuchert 2007a) with approximately 25 valid species (Bouillon *et al.* 2006). One species has been included in a molecular phylogenetic analysis (Collins *et al.* 2006a). No putative synapomorphies are known in the hydroid stage. The family is distinguished by relatively large medusae that possess a large number of (greater than 16) radial canals (Cornelius 1992).

**Aglaopheniidae Agassiz, 1862** comprises eight genera (Schuchert 2007a) and approximately 250 valid species (Bouillon *et al.* 2006). Eleven species, including four genera, have been included in molecular phylogenetic analyses; their monophyly was strongly supported (Leclère *et al.* 2007). The family is distinguished by one median nematotheca below each hydrotheca and a pair of lateral nematotheca fused with the hydrotheca. Fused lateral nematotheca are thought to be a plesiomorphy for the family (Leclère *et al.* 2007).

**Barcinidae Bouillon, Gili, Pagès, Palanques & Puig, 1999** is a monospecific family (Gili *et al.* 1999) whose sole member has not been included in molecular phylogenetic analyses. Hydroids of the family are unknown; medusae are distinguished by the presence of closed statocysts and adaxial ocelli (Gili *et al.* 1999).

**Blackfordiidae Bouillon, 1984** is a monogeneric family (Schuchert 2007a) with three valid species (Bouillon *et al.* 2006). A single representative has been included in molecular phylogenetic analyses. No puta-

tive synapomorphies are known in the hydroid stage; the medusae have four long fluted lips and numerous marginal tentacles with endodermal cores that extend into the mesoglea of the bell.

**Campanulinidae Johnston, 1836** comprises 13 genera (Schuchert 2007a) and approximately 40 valid species (Bouillon *et al.* 2006). None of its species have been included in molecular phylogenetic analyses. No putative synapomorphies are known in the hydroid stage and the group is almost certainly a polyphyletic assemblage of genera that have a tubular hydrotheca with a pointed, segmental or pleated operculum, and that lack a medusa stage (Cornelius 1992; Bouillon *et al.* 2006).

**Cirrhoveniidae Bouillon, 1984** is a monogeneric family (Schuchert 2007a) with two valid species (Bouillon *et al.* 2006). Neither of its species have been included in molecular phylogenetic analyses, and no putative synapomorphies have been proposed for either the hydroid or medusa stage.

**Clathrozoidae Hirohito, 1967** comprises two monospecific genera (Bouillon *et al.* 2006), neither of which have been included in molecular phylogenetic analyses. Members of this family are distinguished by a hydroid skeleton consisting of anastomosed chitinous stolons.

**Dipleurosomatidae Boeck, 1866** comprises four genera and approximately eight valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and no putative synapomorphies are known in the hydroid stage. Medusae of this family are distinguished by branched or irregularly arranged radial canals and a manubrium with a narrow base.

**Eirenidae Haeckel, 1879** comprises nine (Schuchert 2007a) or 10 genera (Bouillon *et al.* 2006) and approximately 65 valid species (Bouillon *et al.* 2006). None of its species have been included in molecular phylogenetic analyses. No putative synapomorphies have been proposed for either the medusa or hydroid stages, the latter of which is recognized by elongate polyps and diminutive or absent hydrothecae.

**Haleciidae Hincks, 1868** comprises four genera (Schuchert 2007a) and approximately 120 valid species (Bouillon *et al.* 2006). Two species representing three genera have been included in molecular phylogenetic analyses, which contradict monophyly of this group, albeit with low support for the nodes separating its representatives (Leclère *et al.* 2007). This family is distinguished by large polyps that are unable to retract into the hydrotheca. The hydrotheca often appears as a collar at the base of the polyp.

**Halopterididae Millard, 1962** comprises 12 genera and approximately 85 valid species (Schuchert 1997; Bouillon *et al.* 2006). Eleven species representing three genera have been included in molecular phylogenetic analyses, which strongly support monophyly of the group (Leclère *et al.* 2007). This family is distinguished by one median nematotheca and a pair of lateral nematotheca associated with each hydrotheca. The hydrothecae are found on stems and terminal branches. These morphological characters are interpreted as plesiomorphies for the family (Leclère *et al.* 2007).

**Hebellidae Fraser, 1912** comprises six genera (Schuchert 2007a) and approximately 40 valid species (Bouillon *et al.* 2006). Two species representing two genera have been included in molecular phylogenetic analyses, which provide low support for monophyly (Leclère *et al.* 2007). Monophyly of Hebellidae (without the genus *Stauroidiscus*, which is sometimes considered to be a part of Laodiceidae) was also supported in a phylogenetic analysis based on morphology (Marques *et al.* 2006). None of its diagnostic characters are unique to the group, many of them being present in members of Lafoeidae or putative outgroups (Marques *et al.* 2006).

**Kirchenpaueriidae Stechow, 1921** comprises five genera (Schuchert 2007a) and 40 valid species (Bouillon *et al.* 2006). Four species from three genera have been sampled for molecular analysis, which strongly support monophyly of the group (Leclère *et al.* 2007). This family is distinguished by having one median nematotheca below each hydrotheca.

**Lafoeidae Agassiz, 1865** comprises nine genera (Marques *et al.* 2006) and approximately 100 valid species (Bouillon *et al.* 2006). A tenth genus, *Billardia*, is sometimes classified in the family (Bouillon *et al.*

2006), but its phylogenetic affinity is unclear. Lafoeidae (excluding *Billardia*) has been shown likely to be monophyletic based on morphology, though putative synapomorphies were dependent on out-group choice (Marques *et al.* 2006). Most species in the family have gonothecae closely packed in a coppinia.

**Laodiceidae Agassiz, 1862** comprises six genera (Schuchert 2007a) and approximately 25 valid species (Bouillon *et al.* 2006). The family has not been the subject of phylogenetic analysis, and no putative synapomorphies are known in the hydroid stage. Medusae of Laodiceidae have marginal cordyli and lack statocysts, but cordyli and cordyli-like structures are known in other families of Leptothecata.

**Lineolariidae Allman, 1864** comprises three genera and four valid species (Bouillon *et al.* 2006). The group has never been the subject of a phylogenetic analysis. Species are recognized by having hydrothecae and gonothecae that are adherent to the substrate for most of their lengths.

**Lovenellidae Russell, 1953** comprises five genera (Schuchert 2007a) and approximately 30 valid species (Bouillon *et al.* 2006). Two representatives from two genera, *Lovenella* and *Eucheilota* (sometimes considered to be in a separate family, Eucheilotidae), have been sampled for molecular data and found to form a strongly supported monophyletic group (Govindarajan *et al.* 2006). Further sampling is needed for a more explicit test of monophyly. The family is distinguished only by medusae characters, including lateral cirri, numerous statocysts, and a short manubrium.

**Malagazziidae Bouillon, 1984** comprises three genera (Schuchert 2007a) and approximately 20 valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of any phylogenetic analyses. No putative synapomorphies are known in the hydroid stage. Medusae of this family have gametogenic tissue completely surrounding the radial canals and tentacle bulbs with adaxial excretory papillae, features that are also exhibited by other leptothecate groups.

**Melicertidae Agassiz, 1862** comprises four genera (Schuchert 2007a) and as many as six valid species (Bouillon *et al.* 2006). One species from the family has been included in molecular phylogenetic analyses, and so monophyly of the group remains untested. Phylogenetic analyses suggest that this family may be the sister taxon to the rest of Leptothecata (Collins *et al.* 2006a). This family is distinguished by the absence of a hydrotheca (though the hydroid is known only for one of the genera), suggesting that the theca may have evolved after the divergence of Melicertidae from the rest of the leptothecates. Medusae are recognized by eight simple or bifurcating radial canals, a manubrium with a broad base, and the absence of cirri, statocysts and cordyli.

**Mitrocomidae Haeckel, 1879** comprises 10 genera (Schuchert 2007a) and approximately 30 valid species (Bouillon *et al.* 2006). The group has never been part of any analysis explicitly assessing its monophyly. Members of the family are distinguished by tubular, sessile hydrothecae in the hydroid stage and by a manubrium attached to the subumbrella along a continuum of the radial canals and open statocysts in the medusa stage. Genera with ocelli associated with open statocysts (*Octogonade*, *Tiaropsidium*, and *Tiaropsis*) are sometimes classified separately in family Triaropsidae (Bouillon *et al.* 2006).

**Octocannoididae Bouillon, Boero & Seghers, 1991** is a monospecific family (Bouillon *et al.* 2006). This family is only known from the medusa stage and is distinguished by multiple club shaped tentaculæ at the bell margin in addition to eight normal tentacles; all have dark pigment spots. The gametogenic tissue is divided into lateral halves along the radial canals.

**Orchistomatidae Bouillon, 1984** is a monogeneric family (Schuchert 2007a) with five valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the family's monophyly has not been tested. Hydroid stages are unknown; medusae are distinguished by a short manubrium, a large gastric peduncle, a mouth with many crenulated lips, adaxial ocelli, and laterally compressed tentacles.

**Phialellidae Russell, 1953** comprises two genera (Schuchert 2007a) and approximately 10 valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses. This family is distinguished by the absence of marginal cirri from the medusa and a crease line at the base of the hydrothecal operculum. It is questionable whether these characters are synapomorphies for the group (Cornelius 1982).

**Plumulariidae McCrady, 1859** comprises six genera (Schuchert 2007a) with approximately 170 valid species (Bouillon *et al.* 2006). Fourteen species representing five genera have been sampled for molecular phylogenetic analysis, which strongly supports monophyly of the group (Leclère *et al.* 2007). The family is distinguished by attributes of the paired nematothecae, which are either absent or never fused with hydrothecae.

**Sertulariidae Lamouroux, 1812** comprises 26 genera (Schuchert 2007a) and approximately 600 valid species (Bouillon *et al.* 2006). Five species representing four genera have been included in molecular phylogenetic analyses, which contradicted monophyly of this group, albeit with low support for the nodes separating the different lineages (Leclère *et al.* 2007). This family is characterized by erect colonies and sessile hydrotheca with a hinged operculum.

**Sugiuridae Bouillon, 1984** is a monospecific family (Bouillon *et al.* 2006) whose sole member has never been included in molecular phylogenetic analyses. No putative synapomorphies are known in the hydroid stage. This family is characterized by medusae with multiple manubria.

**Syntheciidae Marktanner-Turneretscher, 1890** comprises three genera (Schuchert 2007a) and approximately 35 valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group's monophyly has not been tested. Species of this family usually have erect colonies that are unbranched or with pinnate stems, with hydrotheca on both sides of the stem.

**Teclaiidae Bouillon, Gili, Pagès, Palanques & Puig, 1999** comprises two genera (Schuchert 2007a), each with a single valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses. The hydroid stage is unknown and the medusae possess marginal tentacles separated by cordiliform structures.

**Thyroscyphidae Stechow, 1920** comprises five genera (Schuchert 2007a) and approximately 20 valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses and the group has not been the subject of a phylogenetic analysis. Members of this family possess an ectodermal annular fold on the polyp, but this feature is also present in some species of Aglaopheniidae and Sertulariidae.

**Tiarannidae Russell, 1940** comprises six genera (Schuchert 2007a) and approximately 15 valid species (Bouillon *et al.* 2006). No representatives have been included in molecular phylogenetic analyses. Medusae of this family are distinguished by having the gametogenic tissue folded on the adradial walls of the manubrium and/or on the perradial manubrial pouches.

#### Suborder Proboscidoidea

Proboscidoidea comprises three families (Schuchert 2007a) and approximately 150 valid species (Bouillon *et al.* 2006). The putative synapomorphy for this suborder is a flared hypostome forming a pregastric cavity. The group was not revealed as monophyletic in the analyses of Govindarajan *et al.* (2006), but this study was not focused on this question and leptothecate taxon sampling was relatively narrow.

#### *Included families*

**Bonneviellidae Broch, 1909** is a monogeneric family (Schuchert 2007a) with approximately 10 valid species (Bouillon *et al.* 2006). Four representatives, only one of which was identified to species, have been

included in molecular phylogenetic analyses. These analyses supported monophyly of the family (Govindarajan *et al.* 2006), but more explicit tests await further sampling. This family has a unique hypostome morphology, with the pregastric cavity separated by the base of the tentacles, projecting into the gastric cavity and fusing to form a ring.

**Campanulariidae Johnston, 1836** comprises 11 genera (Schuchert 2007a) with approximately 140 valid species (Bouillon *et al.* 2006). Forty six species representing eight genera have been sampled for molecular phylogenetic analysis. The results fail to support monophyly of the group: members of Bonneviellidae nest inside Campanulariidae (Govindarajan *et al.* 2006). Members of Campanulariidae are distinguished by the campanulate-shaped skeleton (theca) surrounding the polyp and a peduncled hypostome. Bonneviellidae does not have this feature.

**Phialuciidae Bouillon, 1984** is a monospecific family (Bouillon *et al.* 2006) whose sole species has not been included in molecular phylogenetic analyses. Hydroids are similar to those of campanulariids, but with a rounded hypostome. Medusae possess rudimentary bulbs between hollow marginal tentacles.

### Order Siphonophorae

Siphonophora Eschscholtz, 1829 comprises 16 families (Schuchert 2007a) and approximately 160 valid species (Dunn *et al.* 2005) divided into three suborders: Calycophorae, Cystonectae, and Physonectae. Molecular phylogenetic analysis strongly support siphonophore monophyly (Collins 2002; Dunn *et al.* 2005). Siphonophores are characterized by their holopelagic, highly polymorphic colonial organization.

#### Suborder Calycophorae

Calycophorae comprises six families and approximately 100 valid species (Pugh 1999). Molecular phylogenetic analyses support monophyly of Calycophorae (Dunn *et al.* 2005). The putative synapomorphies for the group are the absences of an apical pneumatophore and palpons (Dunn *et al.* 2005).

#### *Included families*

**Abylidae Agassiz, 1862** comprises five genera and approximately 10 valid species (Pugh 1999). Only a single representative has been included in molecular phylogenetic analyses (Dunn *et al.* 2005), and no explicit tests of the group's monophyly have been conducted. This family is distinguished by having two nectophores, with the posterior one lacking a somatocyst.

**Clausophyidae Totton, 1954** comprises four genera and approximately 10 valid species (Pugh 1999). Three species representing two genera have been sampled for molecular analysis, the results of which support monophyly of the group (Dunn *et al.* 2005). This family is distinguished by the possession of two nectophores, each of which has a somatocyst.

**Diphyidae Quoy & Gaimard, 1827** comprise eight genera and approximately 50 valid species (Pugh 1999). Seven representatives, representing six genera, have been included in molecular phylogenetic analyses, the results of which strongly support monophyly of the group (Dunn *et al.* 2005). The possession of two dissimilar nectophores appears to be a synapomorphy for the group (Dunn *et al.* 2005).

**Hippopodiidae Kölliker, 1853** comprises two genera and five valid species (Pugh 1999). Four representatives including species from both genera have been included in molecular phylogenetic analyses, the results of which strongly support monophyly of the group (Dunn *et al.* 2005). This family is distinguished by multiple nectophores of one type and the absence of bracts; both of these features appear to be synapomorphies for this group (Dunn *et al.* 2005).

**Prayidae Kölliker, 1853** comprises seven genera and 12 valid species (Pugh 1999). Six species from five genera have been included in molecular phylogenetic analyses. The results of these phylogenetic analyses contradict monophyly of the group; Hippopodiidae nests within Prayidae (Dunn *et al.* 2005). The family is distinguished by two relatively large nectophores.

**Sphaeronectidae Huxley, 1859** is a monogeneric family with four valid species (Pugh 1999). A single representative has been included in molecular phylogenetic analyses and no explicit tests of the group's monophyly have been conducted (Dunn *et al.* 2005). This family is distinguished by a single spherical nectophore.

#### Suborder Cystonectae

Cystonectae comprises two families and five recognized species (Pugh 1999). Molecular phylogenetic analyses demonstrate that Cystonectae is monophyletic and the sister group to all other siphonophores (Dunn *et al.* 2005). The putative synapomorphy of Cystonectae is the absence of a nectosome or bracts and a relatively large pneumatophore.

#### *Included families*

**Physaliidae Brandt, 1835** is a monospecific family (Pugh 1999). Although its sole species has been included in molecular phylogenetic analyses (Dunn *et al.* 2005; Collins *et al.* 2006a), there have been no explicit investigations of cryptic diversity within the group. This family is distinguished by a large, horizontal pneumatophore.

**Rhizophysidae Brandt, 1825** comprises two genera and four recognized species (Pugh 1999). Two species have been sampled for molecular analysis, the results of which do not support monophyly: Physaliidae nests within this group (Dunn *et al.* 2005). Further sampling is needed to test this result. This family is distinguished by an apical and vertical pneumatophore.

#### Suborder Physonectae

Physonectae comprises seven families and approximately 50 valid species (Pugh 1999). The putative synapomorphies are the relatively small apical pneumatophore and a series of identical nectophores located beneath the pneumatophore. Molecular phylogenetic analyses suggest that the Physonectae is paraphyletic with respect to Calycophorae (Collins 2002; Dunn *et al.* 2005).

#### *Included families*

**Agalmatidae Brandt, 1835** comprises nine genera and approximately 25 valid species (Pugh 1999). Nine species representing three genera have been included in molecular phylogenetic analyses, the results of which contradict monophyly and indicate that Agalmatidae is a polyphyletic assemblage (Dunn *et al.* 2005). There are no unique morphological features for this family.

**Apolemidae Huxley, 1859** comprises three monospecific genera (Pugh 1999). Four representatives from one genus (*Apolema*) have been included in molecular phylogenetic analyses, although none were identified to species. The results of these phylogenetic analyses strongly support monophyly of the group (Dunn *et al.* 2005), although further sampling is needed to explicitly test this hypothesis. This family is distinguished by a hollowed nectophore that forms a pair of large axial wings.

**Athorybiidae Huxley, 1859** comprises two genera and three known species (Pugh 1999). Two representatives have been included in molecular phylogenetic analyses, but these represent Atlantic and Pacific populations of the same species. Phylogenetic analyses support monophyly (Dunn *et al.* 2005), but further taxon sampling is needed to test this hypothesis. The family is distinguished by the absence of a nec-

tophore, a feature which appears to be a synapomorphy for this group (Dunn *et al.* 2005).

**Forskaliidae Haeckel, 1888** is a monogeneric family with six valid species (Pugh 2003). Six representatives of four species have been included in molecular phylogenetic analyses; one of the species (*Forskalia edwardsi*) was sampled from two locations in the Pacific and one from the Atlantic. Phylogenetic analyses support monophyly (Dunn *et al.* 2005). The putative synapomorphy for the group is the possession of four types of bracts (Dunn *et al.* 2005).

**Physophoridae Eschscholtz, 1829** is a monospecific family (Pugh 1999) whose sole species has been included in molecular phylogenetic analyses (Dunn *et al.* 2005). One of the distinguishing features of the species, short stemmed physonects, is a pleisiomorphy (Dunn *et al.* 2005).

**Pyrostephidae Moser, 1925** comprises two genera and four valid species (Kirkpatrick & Pugh 1984). Two species of *Bargmannia* have been included in molecular phylogenetic analyses; the results of these analyses support monophyly (Dunn *et al.* 2005). This family is distinguished by long stems, dioecy, and the absence of palpons. The absence of palpons is likely a synapomorphy that arose convergently in Calycophorae (Dunn *et al.* 2005); the other traits are pleisiomorphies. Although it has not been tested explicitly, the molecular evidence and the absence of palpons suggest that monophyly of this group is likely.

**Rhodaliidae Haeckel, 1888** comprises seven genera and 10 valid species (Pugh 1983). Only a single representative has been included in molecular phylogenetic analyses (Dunn *et al.* 2005) and no explicit tests of the group's monophyly have been conducted. The distinguishing features of the family are short stemmed physonects and a benthic life style.

#### SUBCLASS TRACHYLINA

The hydrozoan subclass Trachylina comprises all species classified in Actinulida, Limnomedusae, Narcomedusae, and Trachymedusae (Schuchert 2007). These four orders presently contain about 150 valid extant species (Bouillon *et al.* 2006).

The phylogenetic hypotheses of Bouillon and Boero (2000) and Marques and Collins (2004) recognize a close relationship between Actinulida, Narcomedusae, and Trachymedusae, all of which are direct developing and have ecto-endodermal statocysts. However, the position of Limnomedusae has been somewhat controversial. Bouillon and Boero (2000) maintain that the presence of a polyp stage in Limnomedusae indicates that it shares a common ancestry with Anthoathecata, Leptothecata, and Siphonophora, but its position was equivocal in cladistic analyses of morphological and life history characteristics (Marques & Collins 2004). Molecular phylogenetic analyses including samples from Limnomedusae, Narcomedusae, and Trachymedusae have provided strong evidence for their close relationship (Collins 2002; Collins *et al.* 2006a). Actinulida has yet to be sampled for molecular data. The clearest diagnostic apomorphy for Trachylina is statocysts of ecto-endodermal origin (Haeckel 1879).

#### Order Actinulida

Actinulida Swedmark & Teissier, 1959 was created for Halammohydridae and Otohydridae, two groups of interstitial species. Integral to their decision was the documentation that species of both groups have direct development via an actinula-like stage. Swedmark and Teissier (1966) regarded this life cycle as ancestral for Hydrozoa, and therefore rejected earlier ideas that Halammohydridae was a derived group of Narcomedusae (Remane 1927). However, subsequent authors have suggested that these animals are most likely descendants of trachylina species with free-swimming medusa stages (e.g., Werner 1965; Salvini-Plawen 1987; Bouillon & Boero 2000; Marques & Collins, 2004). Trachymedusae and Narcomedusae are also direct developers with

ontogenetically similar (ecto-endodermal) statocysts. However, characters affiliating the two actinulid families to any particular group within Trachylina, or even to each other, are lacking.

#### *Included families*

**Halammohydridae Remane, 1927** is a monogeneric family with ten valid species (Bouillon *et al.*, 2006), all of which live interstitially. No species of this family have ever been included in a phylogenetic analysis. Members of Halammohydridae possess a distinctive aboral adhesive organ, a nerve ring, and two amphicoronate whorls of aboral tentacles; these unique features suggest that the group is monophyletic.

**Otohydridae Swedmark & Teissier, 1958** is a monogeneric family with two valid species (Bouillon *et al.* 2006). Its members have not been included in any phylogenetic analyses. The species of Otohydridae are readily distinguished from those of Halammohydridae because they lack a nerve ring and have one whorl of dimorphic oral tentacles.

#### Order Limnomedusae

Limnomedusae Kramp, 1938 has a complicated taxonomic history. Kramp (1938; Browne & Kramp 1939) erected the taxon for the hydrozoan families Moerisiidae, Olindiasidae (= Olindiidae), and Proboscidactylidae to accommodate species with a biphasic life-cycle that did not readily fit in the Anthoathecata (=Anthomedusae or Athecata) because their medusae had either ecto-endodermal statocysts or gametogenic tissue along their radial canals, and also failed to fall in Leptothecata (=Leptomedusae or Thecata) because their polyps were not covered by a theca. Naumov (1960) added Monobrachiidae, whose species meet the criteria above. Two other families, Armorhydridae and Microhydrulidae, have also been classified within Limnomedusae, for lack of better alternatives (Bouillon 1985).

Broader considerations of more characteristics, including the cnidom, have indicated that Moerisiidae has a closer relationship to members of the anthoathecate group Capitata (Rees 1958; Petersen 1990). Likewise, the absence of statocysts and the presence of desmonemes strongly suggest that Proboscidactylidae shares a recent common ancestor with anthoathecate species classified in Filifera (Edwards 1973; Schuchert 1996). Molecular data have confirmed that Moerisiidae and Proboscidactylidae are more closely related to anthoathecate species than they are to those of Limnomedusae (Collins 2002; Collins *et al.* 2006a). Thus, Limnomedusae is presently limited to Armorhydridae, Microhydrulidae, Monobrachiidae, and Olindiasidae.

The molecular phylogenetic analyses of Collins *et al.* (2006a) included representatives of Monobrachiidae and Olindiasidae. These analyses did not support monophyly of the order, instead favoring (but with modest support values) the hypothesis that the group is a paraphyletic grade at the base of Trachylina. Additionally, these data provided relatively strong support for the hypothesis that the trachymedusan family Geryoniidae is derived within Limnomedusae. It is unclear precisely why Armorhydridae is included in Limnomedusae, as it appears to not share any putative synapomorphies with other limnomedusans. Their medusae, which inhabit the interstices of coarse sediments, differ from those of other limnomedusans by the presence of hollow tentacles and the absence of radial canals (gametes borne on the manubrium), statocysts, or other sense organs. The position of Microhydrulidae in Limnomedusae is also somewhat tentative. Adult stages of species of Microhydrulidae are unknown. Their polyps are solitary, minute, without tentacles, and armed with just a general nematocyst type, microbasic euryteles.

#### *Included families*

**Armorhydridae Swedmark & Teissier, 1958** is a monospecific family whose single valid species, *Armorhymedra janowiczi*, lives interstitially in coarse sediments. This species has never been included in a population-level analysis, which could presumably reveal cryptic diversity.



**Microhydrulidae Bouillon & Deroux, 1967** comprises two genera and three described species, all considered valid (Bouillon *et al.* 2006). Its members have not been included in any phylogenetic analyses. The species are only known from the minute polyp stage (< 500 µm), which are distinguished from those of other Limnomedusae by their lack of tentacles and mouths. There is no evidence of monophyly.

**Monobrachiidae Naumov, 1960** is a monogeneric family containing three valid species (Bouillon *et al.* 2006). Only a single species has been sampled for molecular data, and the species have never been the subject of a phylogenetic analysis. The family can be differentiated from other limnomedusans by its polymorphic hydroid colonies, which live on bivalve molluscs. Monophyly of the family is likely.

**Olindiasidae Haeckel, 1879** comprises 16 genera (Schuchert 2007) and approximately 40 valid species (Bouillon *et al.*, 2006). Six species and genera were included in the analyses of Collins *et al.* (2006a); results of these analyses indicate that the family is paraphyletic, having given rise to the trachymedusan family Geryoniidae. Olindiasidae differs from Geryoniidae only in the presence of a polyp stage, so non-monophyly of the group is not surprising.

### Order Narcomedusae

Narcomedusae Haeckel, 1879 currently contains four families (Schuchert 2007): Aeginidae, Cuninidae, Solmarisidae, and Tetraplatiidae. Investigations of narcomedusan relationships are still in their infancy. The most detailed published analysis is that of Collins *et al.* (2006b), which included representatives of Aeginidae, Cuninidae, and Tetraplatiidae and corroborated the narcomedusan affinities suggested by Hand (1955) for the worm-shaped *Tetraplatia*. Molecular data consistently support the monophyly of Narcomedusae (Collins 2002; Collins *et al.* 2006a, b). Even as taxon sampling increases in such studies, monophyly of Narcomedusae is likely to be upheld because its members share a number of distinctive features that are likely to be synapomorphies. For instance, the oral-aboral axes in adult medusae are derived from the transverse axes of their respective planulae (Bouillon 1987) and the tentacles arise from the exumbrella rather than at the margin.

#### *Included families*

**Aeginidae Gegenbaur, 1857** comprises six genera (Schuchert 2007) with fewer than ten accepted species (Bouillon *et al.* 2006). Only two species have been sampled for molecular data, and these do not form a clade (Collins *et al.* 2006b) because *Tetraplatia* is derived within them. The paraphyly of Aeginidae is not surprising, as it is differentiated from Cuninidae and Solmarisidae by the presence of interradial manubrial pouches that are very similar to pouches that run up into the interradially located flying buttresses of *Tetraplatia*. This character may be a synapomorphy of Aeginidae plus Tetraplatiidae.

**Cuninidae Bigelow, 1913** comprises four genera (Schuchert 2007) and approximately 20 valid species (Bouillon *et al.* 2006). A single species has been sampled for molecular data (Collins *et al.* 2006b); no test of the monophyly of the group has been conducted. Cuninidae is distinguished from other narcomedusans by manubrial pouches located in the perradii.

**Solmarisidae Haeckel, 1879** comprises two genera (Schuchert 2007) and approximately 10 valid species (Bouillon *et al.*, 2006). No representatives have been sampled for molecular data and monophyly of the group has not been assessed. Solmarisidae is separated from other narcomedusans because its species lack manubrial pouches.

**Tetraplatiidae Schuchert, 2007** is a monogeneric family containing two valid species (Rees & White 1957), one of which has been sampled for molecular data (Collins *et al.* 2006b). While monophyly of the group has not been tested, the distinctive morphology of its members (Hand 1955; Rees & White 1957) would suggest that the species of *Tetraplatia* have a single evolutionary origin.

## Order Trachymedusae

As presently constituted, Trachymedusae Haeckel, 1866 contains five families (Schuchert 2007): Geryoniidae, Halicreatidae, Petasidae, Ptychogastridae, and Rhopalonematidae. No detailed analyses of their relationships have been conducted. Only four species, representing Geryoniidae, Halicreatidae, and Rhopalonematidae, have been sampled for molecular data (Collins *et al.* 2006a). These data indicate that the group may be diphyletic; a representative of Geryoniidae was found to have a close relationship to some members of Limnomedusae. As a practical matter, the two groups are difficult to distinguish. Members of Geryoniidae, like other trachymedusans and unlike limnomedusans, lack polyp stages. However, geryonids share several characters (e.g., centripetal canals, hollow marginal tentacles, and four or six radial canals) with members of Limnomedusae. Disentangling the relationships among limnomedusans and trachymedusans is clearly a priority for future studies in trachyline systematics.

### *Included families*

**Geryoniidae Péron & Lesueur, 1810** comprises two monospecific genera (Bouillon *et al.* 2006). Each of the geryonid species has a cosmopolitan distribution and neither has been the subject of population-level genetic studies, which could detect cryptic diversity. The two genera are distinctive, differing mainly in symmetry: one is four-parted and the other six-parted. Monophyly is likely.

**Halicreatidae Fewkes, 1886** comprises five genera (Schuchert 2007) and approximately 10 valid species (Bouillon *et al.* 2006). A single representative has been sampled for molecular data (Collins *et al.* 2006a). Halicreatidae is distinguished from other trachymedusans by a wide circular manubrium that lacks lips, and tentacles that are stiff distally.

**Petasidae Haeckel, 1879** comprises two monospecific genera (Bouillon *et al.* 2006; Schuchert 2007). No representatives have been sampled for molecular data and monophyly of the group has not been assessed. Petasidae is distinguished from other trachymedusans in having tentacles that terminate in a club-shaped knob of cnidae and four radial canals (shared with *Liriope* of Geryoniidae and *Varitentaculata* of Halicreatidae).

**Ptychogastridae Mayer, 1910** comprises two genera (Schuchert 2007) and three valid species (Bouillon *et al.* 2006). No representatives have been sampled for molecular data and monophyly of the group has not been assessed. Members of Ptychogastridae are benthopelagic and distinguished from other trachymedusan families by having adhesive discs on some tentacles.

**Rhopalonematidae Russell, 1953** comprises 16 genera (Schuchert 2007) and approximately 35 valid species (Bouillon *et al.* 2006). Two species have been sampled for molecular data (Collins *et al.* 2006a), and although they did not form a clade, no convincing test of the group's monophyly has been conducted. The family is distinguished from other trachymedusans by the possession of eight (usually) narrow radial canals and a narrow manubrium that terminates in a mouth with distinct lips.

## **CLASS SCYPHOZOA**

M.N. Dawson

Class Scyphozoa presently contains approximately 200 extant morphospecies (Mianzan & Cornelius 1999), but the true diversity of the group is likely to be at least two times greater (Dawson 2004). Thus, current estimates of species richness in any higher taxon are best viewed as an estimate. Scyphozoa has historically included five morphogroups, ascribed ordinal status but known colloquially as coronates, cubomedusae, rhizostomes, semaestomes, and stauromedusae (e.g., Mayer 1910; Kramp 1961). However, many investigators using morphological data (e.g., Thiel 1966; Russell 1970; Werner 1973; Marques & Collins 2004; see

also Arai 1997) determined that Class Scyphozoa is composed of only coronates, rhizostomes, and semaestomes. This interpretation has been corroborated by the consensus of recent molecular analyses (Collins 2002; Collins *et al.* 2006a), Cubozoa and Staurozoa are now recognized as distinct classes. Moreover, molecular analyses also have indicated that Scyphozoa comprises only two monophyletic groups: Order Coronatae and Order Discomedusae. Discomedusae comprises the semaestomes, which are paraphyletic with respect to a monophyletic Rhizostomeae (Collins 2002; Dawson 2004; Collins *et al.* 2006a).

The life-history of almost all Scyphozoa includes a sexually reproducing planktonic medusoid phase (absent in Cassiopeidae) alternating with an asexually reproducing benthic polypoid phase (absent in a handful of polyp-less deep-water medusae). Scyphozoa are distinguished from other Medusozoa by the presence of polydisc strobilation in metamorphosing polyps (a pattern of strobilation that is further modified in some rhizostomes), rhopalia (as opposed to rhopaloids or complex eyes), and ephyrae (Marques & Collins 2004; Collins *et al.* 2006a).

The current operational classification for Scyphozoa is therefore a somewhat cumbersome mix of ordinal and higher taxonomic groupings based on a molecular and morphological consensus (e.g., Thiel 1966; Russell 1970; Werner 1973; Arai 1997; Collins 2002; Dawson 2004; Marques & Collins 2004; Collins *et al.* 2006a) coupled with the sub-ordinal and family-level treatment of Kramp (1961) used by Russell (1970) and Mianzan and Cornelius (1999). The contribution of analyses of the polyps to systematic classification within Scyphozoa remains practically negligible, with some notable exceptions (e.g., Jarms *et al.* 2002).

### Order Coronatae

Coronatae Vanhöffen, 1892 comprises many deepwater (three families exclusively) and some shallow-water species (all or a fraction of species in the three remaining families; Jarms *et al.* 2002). Coronates possess three synapomorphies that distinguish them from other scyphozoans: a coronal furrow, a coronate pedalum, and oocytes that develop without accessory pigments (Marques & Collins 2004). Molecular analyses including representatives of as many as four coronate families support monophyly of Coronatae (e.g. Collins 2002; Dawson 2004; Collins *et al.* 2006a). However, little is known about many of the medusae that inhabit deepwater and the morphological characters listed by Kramp (1961) distinguish some families poorly.

#### *Included families*

**Atollidae Bigelow, 1913** is a monogeneric family composed of six valid species that inhabit the mesopelagic zone. Medusae have more than eight rhopalia alternating with an equal number of tentacles; the marginal lappets are twice as numerous as the tentacles (Kramp 1961).

**Atorellidae Vanhöffen, 1902** is a monogeneric family composed of five valid species. Medusae have six rhopalia.

**Linuchidae Haeckel, 1879** is composed of two genera with four valid species, all of which are found in tropical shallow waters. Kramp (1961) considered the monospecific genus *Linantha* doubtful.

**Nausithoidae Bigelow, 1913** comprises three genera with 22 valid species. Medusae have eight rhopalia, eight tentacles, 16 marginal lappets, and 16 radiating stomach pouches (Kramp, 1961). Preliminary molecular analyses suggest that Nausithoidae may be polyphyletic (Dawson 2004).

**Paraphyllinidae Maas, 1903** is a monogeneric family comprising three valid species. Medusae in this family have four interradial rhopalia with four or more tentacles (Kramp 1961). All exclusively inhabit deepwater.

**Periphyllidae Haeckel, 1880** comprises four genera and seven valid species. Medusae in this family have four interradial rhopalia with four to 28 tentacles (Kramp 1961). All exclusively inhabit deepwater.

## SUBCLASS DISCOMEDUSAE

Discomedusae are distinguished from coronates in having heterotrichous anisorhiza nematocysts, podocysts, complex radial canals, and a partially present circular canal (Marques & Collins, 2004), although the complex radial canal is a homoplasy (also being present in some hydromedusae) and medial circular canals are prominent in some rhizostomes.

### Order Semaestomeae

Within Discomedusae, three genera constitute a group, traditionally known as order Semaestomeae Agassiz, 1862, which is probably paraphyletic with respect to Order Rhizostomeae. The semaestomes are distinguished from rhizostomes by two homoplasies (loss of desmocytes, shared with Staurozoa; presence of glandular cells, shared with Anthozoa and Hydrozoa) and a synapomorphy (presence of nerve cells in the planulae; Marques & Collins 2004).

#### *Included families*

**Cyaneidae Agassiz, 1862** comprises three genera, one distributed globally in shallow-water, another in the Southern Ocean (Larson 1986), and the third in low-to-mid latitude Atlantic and adjacent basins, with approximately 20 recognized morphospecies. The cyaneid medusae are the only Discomedusae having tentacles originating on the subumbrellar surface of the bell at some distance inside of the bell margin.

**Pelagiidae Gegenbaur, 1856** comprises three genera (Kramp 1961) and 15-20 recognized morphospecies. Cladistic analyses of morphological variation indicate that traditionally recognized genera are likely polyphyletic (Gershwin & Collins 2002). Pelagiidae are discomedusae with completely separated but unbranched gastric pouches and long, pointed, folded oral arms (Kramp 1961).

**Ulmaridae Haeckel, 1879** comprises 14 genera and approximately 40 valid species. Slightly more than one-third are in the genus *Aurelia* and are currently identifiable only using molecular comparisons (e.g., Dawson 2003, Dawson *et al.* 2005), although many may represent previously described morphospecies (e.g., Mayer 1910). Many of the remaining species are in monospecific genera of deepwater medusae. Ulmarid medusae have simple or branched radial canals and a ring canal, which distinguish them from all other semaestomes (but not from all rhizostome medusae).

### Order Rhizostomeae

The most diverse order of Scyphozoa, Rhizostomeae Cuvier, 1799 is a monophyletic clade according to phylogenetic analyses of DNA sequence data (Dawson 2004) and is often distinguished from other Discomedusae by monodisc strobilation (although this is not diagnostic of all species in the clade), having oral arms that bear suctorial mouths and are fused proximally, and the absence of tentacles on the bell margin (a feature shared with some deepwater semaestomes). Kramp (1961), following Stiasny (1921) separated Rhizostomes into suborders and superfamilies in addition to the more standard Linnaean ranks. The phylogeny implied by Stiasny's (1921) taxonomy is largely supported by patterns of development (Holst *et al.* 2007) and phylogenetic analyses of DNA sequence from five families representing all superfamilies and suborders (Daryanabard & Dawson, in press). Stiasny's (1921) taxonomy therefore remains the most current (Mianzan & Cornelius 1999) and so is presented below without further embellishment (see Kramp 1961 for more details).

## Suborder Kolpophorae

**Cassiopidae Agassiz, 1862** is a monogeneric family comprising 10 species.

**Cepheidae Agassiz, 1862** comprises four genera and 16 species.

**Mastigiidae Stiasny, 1921** comprises three genera and 14 species.

**Thysanostomatidae Gegenbaur, 1857** is a monogeneric family with three species.

**Versurigidae Gegenbaur, 1857** is a monospecific family.

## Suborder Daktyliophorae

**Lychnorhizidae Haeckel, 1880** comprises three genera and six species.

**Catostylidae Gegenbaur, 1857** comprises six genera and 24 species.

**Lobonematidae Stiasny, 1921** comprises two genera and five species.

**Rhizostomatidae Cuvier, 1799** comprises four genera and 11 species.

**Stomolophidae Haeckel, 1880** is a monogeneric family with two species.

## CLASS STAUROZOA

A.G. Collins

Staurozoa is the most recently designated class of phylum Cnidaria (Marques & Collins 2004). The primary justification for its creation was that order Stauromedusae failed to form a clade with the other scyphozoan taxa in cladistic analyses of morphology and life history characteristics (Marques & Collins 2004), or in molecular phylogenetic analyses (Collins 2002). The cladistic analysis of Marques and Collins (2004) included a problematic extinct group, Conulata, which had a sister group relationship to Stauromedusae in their analyses. The class Staurozoa was erected to contain both of these groups. Subsequent work refining the character scoring for Conulata suggested that these enigmatic fossils are more likely to share a common ancestry with Scyphozoa than with Stauromedusae (Van Iten *et al.* 2006), contradicting the original concept of Staurozoa. Nevertheless, the cladistic analysis of Van Iten *et al.* (2006) and further phylogenetic research based on molecular sequence data (Collins & Daly 2005; Collins *et al.* 2006a) have suggested that Stauromedusae may be the sister group to all other medusozoans. In terms of extant diversity, Staurozoa is equivalent to the order Stauromedusae.

### Order Stauromedusae

The approximately 50 valid species of Stauromedusae Haeckel, 1879 are currently classified in two suborders, Cleistocarpida and Eleutherocarpida (Mills 2007). Only preliminary results from ongoing studies of the systematics of Stauromedusae have been published (Collins & Daly 2005; Collins *et al.* 2006). Thus far, six species of Stauromedusae, representing both suborders and three of the six families, have been sampled for molecular data. These data strongly support monophyly of the sampled species (Collins & Daly 2005; Collins *et al.* 2006a).

As benthic medusozoans, staurozoans are quite distinctive. Several likely synapomorphies of the clade are listed by Collins and Daly (2005), including eight adradial clusters of capitate tentacles and non-ciliated creeping planulae. Families and genera of Stauromedusae are recognized by a combination of characters (Uchida 1929; Kramp 1961; Larson & Fautin 1989; Kikinger & Salvini-Plawen 1995), e.g., with or without a claustrum, peduncle having one or four chambers, peduncle having four intramesogleal muscles or not, coro-

nal muscle being discontinuous in each adradius or unbroken, possession of eight perradial and interradial marginal anchors, primary tentacles, or none. While genera appear to be well defined, the families and suborders seem to be confused.

#### Suborder Cleistocarpida

Cleistocarpida comprises two families, Craterolophidae and Depastridae. The presumed synapomorphy of the suborder is the claustrum, tissue that transversely divides the four gastric pockets. The only explicit tests of the group's monophyly were based on molecular data from two cleistocarpid representatives, each representing one of the families (Collins & Daly 2005; Collins *et al.* 2006a). Monophyly of Cleistocarpida is contradicted by these data. The claustrum, a relatively complex feature (Berrill 1963), appears to be derived independently in different groups of Stauromedusae.

#### *Included families*

**Craterolophidae Uchida, 1929** is a monogeneric family with two valid species (Mills 2007). One species of Craterolophidae has been sampled for molecular data and no explicit test of the group's monophyly has been conducted. Members of this family are distinguished from other cleistocarpids by the lack of primary tentacles in the perradii and interradii and the absence of longitudinal muscles in the peduncle.

**Depastridae Haeckel, 1879** comprises four genera and approximately 10 valid species (Mills 2007). Only one species has been sampled for molecular data, and species of the family have never been the subject of a phylogenetic analysis. The family can be differentiated from other cleistocarpids by the presence of four longitudinal muscles running the length of the peduncle and primary perradial and interradial tentacles (Larson & Fautin 1989).

#### Suborder Eleutherocarpida

Eleutherocarpida is distinguished from Cleistocarpida by the lack of a claustrum (Mills 2007). Phylogenetic assessments of Eleutherocarpida are still in their infancy: only members of Lucernariidae have been sampled for molecular data. Analyses of these data suggest that the suborder does not form a clade, and therefore the lack of a claustrum is not a synapomorphy of the group (Collins & Daly 2005; Collins *et al.* 2006a).

#### *Included families*

**Kishinouyeidae Uchida, 1929** comprises three genera and approximately 10 species (Mills 2007). No representative from this family has been included in a phylogenetic analysis and its monophyly is untested. The one potential synapomorphy of the group is the lack of muscles in the peduncle.

**Kyopodiidae Larson, 1988** is a monospecific family. Its sole species has never been included in a population-level analysis, which could presumably reveal cryptic diversity. Its morphology is highly unusual within Stauromedusae: the calyx is tiny in comparison with the peduncle, and the gametes and gastric cavity reside at the base of the peduncle (Larson 1988). Even if further diversity is revealed in the family, Kyopodiidae is likely to be monophyletic.

**Lipkeidae Vogt, 1887** is a monogeneric family with three species. No representative from this family has been included in a phylogenetic analysis and its monophyly is untested. Its species are distinguished from other Eleutherocarpida by their lack of anchors or papillae and their possession of eight adradial arms bearing either rudimentary or no secondary tentacles (Kramp 1961). The peduncle is single chambered, with muscles, and the coronal muscle is unbroken.

**Lucernariidae Johnston, 1847** is the most diverse family of Stauromedusae, comprising four genera and approximately 20 valid species (Mills 2007). Four species (one only identified to genus) representing two genera have been sampled for molecular data (Collins & Daly 2005; Collins *et al.* 2006a); the results of these analyses strongly contradict monophyly of the group. Of the characters typically used in classifying Eleutherocarpida, the only one shared by members of Lucernariidae is the possession of muscles throughout the length of the peduncle.

## Acknowledgements

This work is part of the Assembling the Cnidarian Tree of Life project, and was supported by NSF EF-0531779 (to P.C., A.G.C. & D.G.F.), 0531763 (to M.D.), 0531570 (to C.S.M.), and 0531735 (to S.L.R.). J.L.S. is supported through NSF-0346483 (VI-EPSCoR program) and M.N.D. is supported through NSF DEB-0717078. Leen van Ofwegen provided helpful comments on octocoral taxonomy. Max Castorani helped organize and proofread literature. We gratefully acknowledge comments from Dale Calder and an anonymous reviewer.

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